Salvador Mandujano
Eduardo J. Naranjo
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Neotropical Mammals

Hierarchical Analysis of Occupancy and Abundance

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Foreword

> The better an ecosystem is known, the less likely it will be destroyed. –Edward O. Wilson; *The Diversity of Life*

A basic understanding of a species' ecological requirements, interactions, and demographic parameters is fundamental both to research into its biology and to its proper conservation management. To put the magnitude of the demands for species management and conservation into perspective, by 2022, 42,100 species were known to be threatened with extinction worldwide, representing 28% of those assessed by the International Union for Conservation of Nature (IUCN 2022).[1] This has led many government agencies and NGOs to become increasingly involved in species management and conservation programs, in which the first questions are always "How many are left?" and "Where are they?" All of us who have ever worked in wildlife management have encountered the need to know (at least) the population sizes of species and their densities. And paradoxically, discovering these most basic parameters has always been extremely difficult, even before tackling the more complex assessments of survival and recruitment rates. Given the difficulties of establishing reliable baselines, it has often been virtually impossible to quantify the effectiveness of any conservation measures that might have been put in place.

What lies at the root of these problems? The main difficulty in estimating the population size of a target species is that the detection probability of individuals is not perfect. And this is not just a problem for elusive species, such as many large carnivores. The reality is that there are very few species and very few situations in which complete counts ("census") can be made. If one tries to make a population estimate based on the individuals detected, the target species population will always be underestimated and the biases will tend to be greater the lower the detectability. Working with a species in the wild requires the use of mathematical modelling tools to estimate the actual situation and enables the study of that species' ecology.

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[1] IUCN (2022) The IUCN red list of threatened species. Version 2022-2. https://www.iucnredlist.org. Accessed on 27 May 2023.

Models are, in essence, a means of estimating what we cannot measure directly. The use of detection probabilities to estimate population size became widespread in the 1970s with the development of capture-recapture (e.g., Otis et al. 1978)[2] and distance sampling methods (e.g., Burnham et al. 1980).[3]

In my opinion, a major advance in the treatment of the probability of detection was the development of the occupancy model presented in the seminal paper by MacKenzie et al. (2003).[4] According to the preface to their subsequent book, *Occupancy Estimation and Modeling: Inferring Patterns and Dynamics of Species Occurrence* (2005),[5] the method crystallized during conversations over several pints of Guinness beer, adding a decidedly extra dimension to their findings! In short, their new model was a hierarchical one based on the simultaneous estimations of occupancy and detection probability in replicate samples. In my opinion, the simplicity and elegance of the occupancy model makes it one of the most attractive models. The concept can be explained thus; a species may or may not be present at a site (an ecological process), and if it is present, it may or may not be detected in a sample (a detection process). In mathematical terms, this is equivalent to two linked binomial models (one for each process), or a conditional detection that can only take place if the species is present. Notwithstanding the recent development of other occupancy-based models, such as multistate, dynamic or multisession, co-occurrence, and community-level models, and their use as proxies for abundance, occupancy models are a fundamental tool that provides improved insight into the ecology of species and communities by allowing the use of descriptor covariates for the ecological process of occupancy, and also the ability to refine this by using descriptor covariates in the detection process. Binomial Poisson or N-mixed models are analogous to occupancy models, but use counts instead of presence-absence data to obtain “abundances” corrected by the probability of detection (Royle and Nichols 2003).[6] Both of these models, and many others (capture-recapture, Jolly-Seber, etc.), have been admirably treated using Bayesian approximations in the iconic book *Bayesian Population Analysis Using WinBUGS. A Hierarchical Perspective* (aka BPA; Kéry and Schaub 2012).[7] The authors encouraged us to “free the modeler in you” with a clear writing style accessible to the practicing ecologist, by using the

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[2] Otis DL, Burnham KP, White GC, Anderson DR (1978) Statistical inference from capture data on closed animal populations. Wildl Monogr 62:3–135. https://doi.org/10.2307/2287873

[3] Burnham KP, Anderson DR, Laake JL (1980) Estimation of density from line transect sampling of biological populations. Wildl Monogr 72:3–202. https://doi.org/10.1126/science.98.2539.185

[4] MacKenzie DI, Nichols JD, Hines JE, Knutson MG, Franklin AB (2003) Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology 84:2200–2207. https://doi.org/10.1890/02-3090

[5] MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey L, Hines JE (2005) Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence. Elsevier.

[6] Royle JA, Nichols JD (2003) Estimating abundance from repeated presence-absence data or point counts. Ecology 84:777–790. https://doi.org/10.1890/0012-9658(2003)084[0777:EAFRPA]2.0.CO;2

[7] Kéry M, Schaub M (2012) Bayesian population analysis using WinBUGS. A hierarchical perspective. Academic Press/Elsevier. https://doi.org/10.1016/B978-0-12-387020-9.00014-6

simplicity of the R (R Core Team 2023)[8] and BUGS languages (Lunn et al. 2000).[9] This work on hierarchical modeling has been further nicely expanded in the two-volume book *Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS* (aka AHM; Kéry and Royle 2022, 2016).[10]

To my mind, the development of spatially explicit capture-recapture (SCR) methods was the next milestone in modern species monitoring modelling. Efford et al. (2004)[11] developed a capture-recapture application (Density) published in the Spanish journal *Animal Biodiversity and Conservation*, which used a maximum likelihood approach incorporating the detector's coordinate information, to use spatial information from the detection process to infer the number and locations of the target species activity centers. More information on this new model was published in another journal in the same year (Efford 2004)[12] and SCR became mainstream. Shortly thereafter, Royle and Young (2008)[13] developed the SCR model within a Bayesian approach using data augmentation. In 2014, Royle et al.[14] published the book *Spatial Capture-Recapture*, which developed and expanded Bayesian approaches to many SCR models. It also incorporates other topics of interest, such as the thought spatially explicit mark-recapture (SMR) models originally described by Sollmann et al. (2013),[15] which combine data from marked individuals with counts from unmarked individuals in estimates.

By incorporating the spatial component of capture-recapture, SCR inherently allows for heterogeneity among individuals in their exposure to detectors, which removes a key source of bias in non-spatial estimators. This, and the explicit modeling of space use in the target species, has allowed a remarkable expansion of population size estimation methods based on SCR, and increased their use including resource selection, connectivity, land planning, and similar studies.

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[8] R Core Team (2023) R: a language and environment for statistical computing. R Foundation for Statistical Computing.

[9] Lunn DJ, Thomas A, Best N, Spiegelhalter DJ (2000) WinBUGS – a Bayesian modelling framework: concepts, structure, and extensibility. Stat Comput 10:325–337. https://doi.org/10.1023/A:1008929526011

[10] Kéry M, Royle JA (2016) Applied hierarchical modeling in ecology: analysis of distribution, abundance and species richness in R and BUGS. Volume 1. Prelude and static models. Academic Press/Elsevier; Kéry M, Royle JA (2022) Applied hierarchical modeling in ecology. Analysis of distribution, abundance and species richness in R and BUGS. Volume 2. Dynamic and advanced models, 1st edn. Academic Press/Elsevier. https://doi.org/10.1016/c2013-0-19160-x

[11] Efford MG, Dawson DK, Robbins CS (2004) DENSITY: software for analysing capture-recapture data from passive detector arrays. Anim Biodivers Conserv 27:217–228.

[12] Efford MG (2004) Density estimation in live-trapping studies. Oikos 106:598–610. https://doi.org/10.1111/j.0030-1299.2004.13043.x

[13] Royle JA, Young KV (2008) A hierarchical model for spatial capture recapture data. Ecology 89: 2281–2289. https://doi.org/10.1890/07-0601.1

[14] Royle JA, Chandler RB, Sollmann R, Gardner B (2014) Spatial capture-recapture. Elsevier, Academic Press, Waltham. https://doi.org/10.1016/B978-0-12-405939-9.00026-8

[15] Sollmann R, Gardner B, Parsons AW, Stocking JJ, Mcclintock BT, Simons TR, Pollock KH, O'Connell AF (2013) A spatial mark-resight model augmented with telemetry data. Ecology 94: 553–559. https://doi.org/10.1890/12-1256.1

Latin American countries are playing a particularly important role in the development and implementation of wildlife monitoring methods that incorporate probability of detection in estimates. In this region, which contains some of the world's most important biodiversity hotspots, many scientists and research groups are using these cutting-edge tools in their monitoring work. This book, edited by my friends Salvador Mandujano, Eduardo J. Naranjo, and Gabriel P. Andrade-Ponce, focuses on some of these studies, bringing together 73 researchers with affiliations in 13 different countries to share their research on both occupancy and abundance studies on Neotropical mammals. I firmly believe that this is an extremely important and useful book, and I am grateful to them for asking me to write this Foreword, and to add the perspective of a Spanish researcher working in quantitative ecology. My long previous career in the daily work of wildlife management in the national parks of Spain has made me aware of the need for accurate and unbiased estimates of flora and fauna populations, and a thorough understanding of the ecological processes and drivers of demographic parameters.

The book is divided into two parts. The first part, Literature Reviews, presents a compendium of global reviews and meta-analyses. The first chapter is devoted to the hierarchical models discussed in the book and is followed by chapters on small felids, pampa mammals, guanaco, primates, and ungulates, with comparisons between different monitoring models and study sites to draw global patterns and conclusions.

The second part, Case Studies, contains case studies on several threatened mammal species: spotted paca (*Cuniculus paca*) in Oaxaca, Mexico; jaguar (*Panthera onca*) in the Venezuelan Llanos; jaguar in the Paraguayan Dry Chaco; Coimbra-Filho's titi monkey (*Callicebus coimbrai*) in the Atlantic Forest, Brazil; mountain tapir (*Tapirus pinchaque*) in northern Peru; wild mammals in two protected areas in the Monte ecoregion of Argentina; and white-tailed deer (*Odocoileus virginianus*) in part of the Tehuacán-Cuicatlán Biosphere Reserve, Mexico. The authors have used non-invasive sampling methods (camera traps, acoustic recordings, and interview surveys) and applied hierarchical models to assess occupancy, distribution, abundance, and resource selection. The last three chapters provide greater focus on descriptions of faunal communities, environmental descriptors, and conditioning factors associated with human activities, such as defaunation processes.

In short, this book provides an excellent and thought-provoking contribution to the application of hierarchical models to the monitoring of Neotropical mammal species in Latin America. Considering the extraordinary biodiversity of this region, and the currently accelerating development of models, it is clear that this book will become a key resource and introduction to the emergence of many exciting future studies to come.

CSIC-IREC, Ciudad Real, Spain José Jiménez García-Herrera

Acknowledgments

The idea of writing this book was born from my experience as coordinator (SM) of various postgraduate courses before the pandemic and which were mainly focused on estimating abundance and occupancy using frequentist and Bayesian models using R. In addition, the idea was strengthened after reviewing the literature on the subject, mainly studies carried out in the Neotropics, and talking with several colleagues on the subject. Thus, initially, I invited Eduardo J. Naranjo, my colleague, and friend from the University at the beginning of the 1980s, so that we could work together as editors of this book. We soon realized the enormous task that this project was going to imply, which is why we decided to invite Gabriel P. Andrade-Ponce as the third editor. So that, together we could tackle the entire process and challenges involved in publishing a book with this purpose.

The original project of the book contemplated including 30 chapters written by many authors with experience in studies with Neotropical mammals and also with experience in applying the hierarchical models that are the focus of this book. All this happened during the years of the terrible pandemic that shook the world. But then came the most complicated part for us as editors when at the beginning of 2022 many of the initial authors apologized to us that they were not finally going to participate because they wanted to recover the time to carry out field trips and other academic activities, and personal which made it difficult for them to continue. Joao's patience and kindness allowed us to negotiate extensions for the delivery of the book. Thus, at the end of 2022 and the beginning of 2023, we managed to integrate 15 chapters written by 73 authors from various countries. We are very grateful to each one of them, but we want to thank the leading authors in charge of coordinating each of their chapters, specifically for their interest, patience, and motivation to contribute to this book. Particularly, Nicolás Gálvez, Tadeu G. de Oliveira, Flávia P. Tirelli, Antonella Panebianco, Anja Hutschenreiter, Antonio Santos-Moreno, Włodzimierz Jędrzejewski, Jeffrey J. Thompson, Igor Pfeifer Coelho, José Luis Mena, and Claudia M. Campos.

Our friend and colleague Rafael Reyna-Hurtado recommended us to contact with Joao Pildervasser, Springer editor, with whom we are grateful for his continuous and timely support, and good advice to improve this book.

Especially, we greatly appreciate José Jimenez for his comments in the Foreword. We admire for his human quality and contribution to hierarchical models. We have learned a lot about HMs through his published articles, classes in courses, and various interactions.

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Part I
Literature Reviews

Chapter 1
Neotropical Mammals and the Analysis of Occupancy and Abundance

Salvador Mandujano, Eduardo J. Naranjo, and Gabriel P. Andrade-Ponce

Abstract Ecology has to do with the number of individuals or species in a biological population or community. Historically, the estimation of population size has been approached with different field methods and statistical analyses. One of the recent approaches to estimating population abundance, occupancy, and density is the use of hierarchical models. Essentially, these models integrate the ecological process (occupancy, abundance, and density) conditional to the observational process (the detection probability, usually <1.0) and estimate parameters through maximum likelihood and/or Bayesian statistical approaches. Occupancy, abundance, and density are central themes in many research projects, theses, and monitoring programs and have direct applications in the conservation and management of Neotropical mammal populations. In this introductory chapter, we briefly address these aspects to put in context the chapters that integrate this book.

Keywords Book organization · Conservation · Hierarchical models · Management · Population ecology

1.1 Introduction

The Neotropics, a biogeographical region comprising Southern Mexico, Central America, South America, and the Antilles, is one of the richest areas of the world in terms of biodiversity, of which mammals constitute an extremely relevant group for ecosystem functioning and human survival. Wild mammals play key roles in the

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dynamics of Neotropical ecosystems as pollinizers, seed dispersers, foliage consumers, and predators (Eisenberg 1989). In addition, mammals have always provided human populations with food, companionship, medicines, hides, bones, tools, ritual objects, and many other material and spiritual goods that have been essential in the development of ancient and modern cultures across the Neotropics (García del Valle et al. 2015).

Over 1600 mammal species representing around a third of the world's diversity of this group have been described in the Neotropical region so far (Burgin et al. 2018). This extraordinary mammalian diversity has developed over a long and complex evolutionary history that began with the extended geographical isolation between North and South America during most of the Cenozoic era (66–0 Ma; Carrillo et al. 2015). Isolation resulted in the evolution and radiation of numerous endemic mammalian taxa in South America (Eisenberg 1989). Although sporadic dispersal events occurred between the two former continents (North and South America), isolation gradually decreased between 7 and 3 Ma, when a connection was established through the Isthmus of Panama, and a major faunal exchange known as the Great American Biotic Interchange (GABI) began to take place (Simpson 1980; Carrillo et al. 2015).

The numerous biomes present in the environmentally heterogeneous Neotropical region have allowed one of the greatest diversifications of terrestrial mammals on the Earth encompassing 15 orders and 62 families of which 29 (46.8%) are endemic to this region (Ojeda 2013). Species groups such as opossums, sloths, armadillos, anteaters, agouties, capybaras, pacas, spiny rats, chinchillas, brad-nosed monkeys, and leaf-nosed bats are exclusive of the Neotropics (Patterson 2020). Rodents (>640 species), bats (>300 spp), and carnivores (>84 spp) are, as in other parts of the world, the most diverse mammalian groups in this biogeographical region (Solari and Martinez-Arias 2014; Patton et al. 2015; Nagy-Reis et al. 2020).

The impressive mammalian diversity of the Neotropics is, however, under pressure because of multiple human-induced processes occurring at different geographical and temporal scales. In the first place, our growing human population and our ever-increasing demands for food, water, energy, transportation, and places to live impose a great challenge for many wild mammals to survive (Ceballos et al. 2020). High rates of deforestation and habitat fragmentation in synergy with overhunting for different purposes (i.e., subsistence, damage control, recreation, and trade) constitute the primary threats for sensitive Neotropical mammals, especially in tropical ecosystems (Dirzo et al. 2022). Large- and medium-sized species living at low-population densities such as carnivores, primates, and some ungulates are often the most affected by these activities. Nonetheless, habitat degradation because of pollution, urbanization, competition with, and predation by, invasive and domestic species may severely compromise the survival of even small mammals (e.g., bats, rodents, shrews, and opossums), particularly if they are endemic or habitat specialist.

Under this complex scenario, many efforts are being made in most Neotropical countries to help save sensitive mammal species from extirpation. The creation and management of different kinds of protected areas, the establishment of biological corridors, hunting regulations for sustainable use, invasive species control, and the improvement of livestock management and agricultural practices to reduce predation and damage are among the most frequent responses so far (Costa et al. 2005; Valdez 2019). These efforts may and should be coupled with ecological and social research focused on assessing the status of threatened populations and their interactions with their habitats and with people. In this context, knowledge about the presence, abundance, and habitat occupancy of wild mammals is key to understanding how conservation and management actions aimed at them may be more effective in the long term. The chapters that make up this book are important contributions in this sense.

The analysis of occupancy and abundance has been widely addressed in studies on Neotropical mammals. In this chapter, we present a preliminary analysis of 309 published studies (2000–2021) on these population attributes. The studies were conducted in 19 countries and 18 Neotropical biomes. Most studies were done in tropical areas of central and southern Mexico, the Atlantic Forest of Brazil and Argentina, the Brazilian, Ecuadorian, and Peruvian Amazon, and Central America (Fig. 1.1). The countries with the highest numbers of published studies were

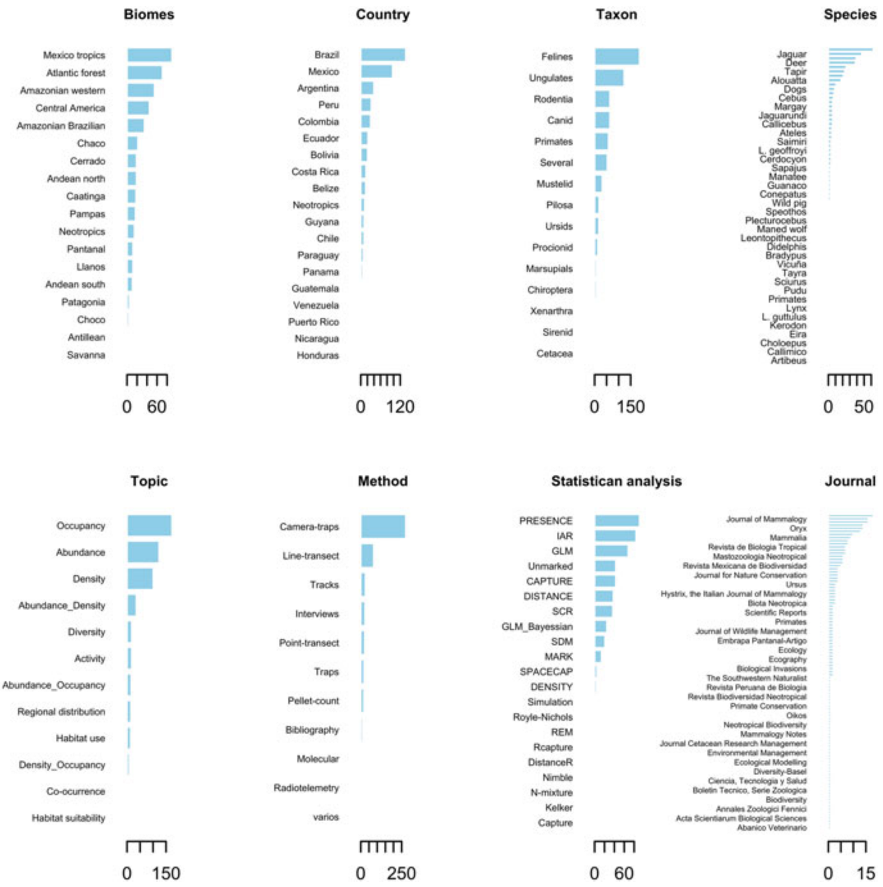

Fig. 1.1 Frequency of the papers ($n = 309$) referring to the study of Neotropical mammals according to the different classifications (biomes, country, bowl, species, topics studied, methods, statistical analyses, and journals in which the works were published)

Brazil and Mexico. The most frequently studied mammal groups were felines, ungulates, rodents (large species), canids, primates, and mustelids (Fig. 1.1). A total of 74 mammal species belonging to 15 families were included in the publications reviewed, with the jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), deer (Cervidae), puma (*Puma concolor*), tapirs (*Tapirus* spp.), peccaries (Tayassuidae), and howler monkeys (*Alouatta* spp.) being the most recurrent. The field methods used to obtain the information were primarily camera-trapping and line transect sampling (Fig. 1.1). The information gathered in the reviewed studies was analyzed through a variety of statistical approaches. Some of them used no hierarchical generalized models and simple calculations of relative abundance indices or photographic rates. Many others included the use of the software PRESENCE, CAPTURE, DISTANCE, and R packages such as "unmarked" and "secr." Finally, the results of the analyzed studies were published primarily in indexed journals (Fig. 1.1). In subsequent chapters, the authors present interesting reviews of assessments on the occupancy, abundance, density, and other population parameters of focal species throughout the Neotropics. The results of those assessments show an increasing interest in applying hierarchical models to estimate such parameters for a growing number of mammals in the region.

1.2 Hierarchical Model Approach for the Analysis of Occupancy and Abundance

Ecology is the study of the factors that determine the distribution and abundance of species (Kéry and Royle 2016, 2020). That is, ecology has to do with the number of individuals or species in a population or community. These three parameters (distribution, abundance, and richness) are frequently the central theme of many thesis projects, scientific investigations, and monitoring programs, and have direct applications in wildlife conservation and management. Classic books have been written on these topics, to name a few: "*The Distribution and Abundance of Animals*" (Andrewartha and Birch 1954), "*Ecology: The Experimental Analysis of Distribution and Abundance*" (Krebs 1978), and "*Analysis of Distribution, Abundance, and Species Richness*" (Kéry and Royle 2016). Furthermore, books dedicated exclusively to the estimation of these parameters have been written. To name a few, "*Distance Sampling: Methods and Applications*" (Buckland et al. 2015), "*Occupancy Estimation and Modeling*" (MacKenzie et al. 2017); and "*Biological Diversity: Frontiers in Measurement and Assessment*" (Magurran and McGill 2010).

Fortunately, one of the most significant advances in the last decade is the development and application of the hierarchical approach to model and analyze the three state variables describing populations and communities. This hierarchical modeling approach is a relatively recent topic and has been addressed in different books by authors such as "*Hierarchical Modeling and Inference in Ecology: The Analysis of Data From Populations, Metapopulations, and Communities*" (Royle and Dorazio 2008), "*Bayesian Population Analysis Using WinBUGS: A Hierarchical Perspective*" (Kéry and Schaub 2012), "*Spatial Capture-Recapture*" (Royle et al. 2014), and "*Applied Hierarchical Modeling in Ecology: Analysis of Distribution, Abundance and Species Richness in R and BUGS*" volume 1 (Kéry and Royle 2016) and volume 2 (Kéry and Royle 2020). The importance and beauty of hierarchical models are that they allow simultaneous modeling of the state or ecological process (abundance, distribution, and/or richness) and the observational process (detection probability). This aspect is central and often overlooked when estimating population/community size without considering at the same time the detection probability, which is usually less than 1.0 (Thompson 2004). The hierarchical approach is a natural way to deal with this estimation problem, differentiating between the contributions of both the state and the observational processes, in addition to incorporating covariates that may be associated with either process.

This book *Neotropical Mammals: Hierarchical Analysis of Occupancy and Abundance* is about distribution and abundance. Occupancy and local abundance are sometimes referred to as density when expressed in terms of habitat area. Both distribution and abundance are fundamentally the results of the underlying spatial point pattern of species (Kéry and Royle 2016). If we were able to observe individuals of a species at a given time in a continuous space, what we would be looking at is a random number of "points" in a series of random locations as a result of the point process. That is, the estimation of the distribution and abundance is only possible when the space is discretized in a finite number of quadrats or sites (Kéry and Royle 2016). Then, the abundance can be expressed as the number of points (N) within each quadrant and the occurrence (z) as the number of quadrants where $N > 0$. To illustrate the relationships between the point pattern, abundance, and distribution, as an example, we used the *simPPe* function of the AHM package (Kéry et al. 2022). This simulation clearly shows how abundance and occurrence vary depending on the intensity (λ, lambda) of the point pattern, and also depending on other factors such as the scale or size of the site or quadrat (Fig. 1.2). These concepts are based on the idea that all individuals (points) are detected. However, in most cases, both the number of animals counted in the sites, as well as the determination of whether the site is truly occupied or not, depend fundamentally on imperfect detection (Denes et al. 2015).

1.3 A Key Aspect: The Probability of Detection

One fact that every wildlife biologist knows is that not all animals that inhabit the study area are counted during samplings. That is, he intuitively recognizes that the probability of detecting all the animals is very seldom equal to one ($p = 1.0$). According to Denes et al. (2015), animals are not fully detected for reasons related to: (1) *Characteristics of the species*: abundance itself (rare species are less detectable), the conspicuousness of the species (size, shape, color), movements (home range, distance, and speed of movement), and foraging habits, among the main ones. (2) *Site characteristics (spatial variation)*: the structure and

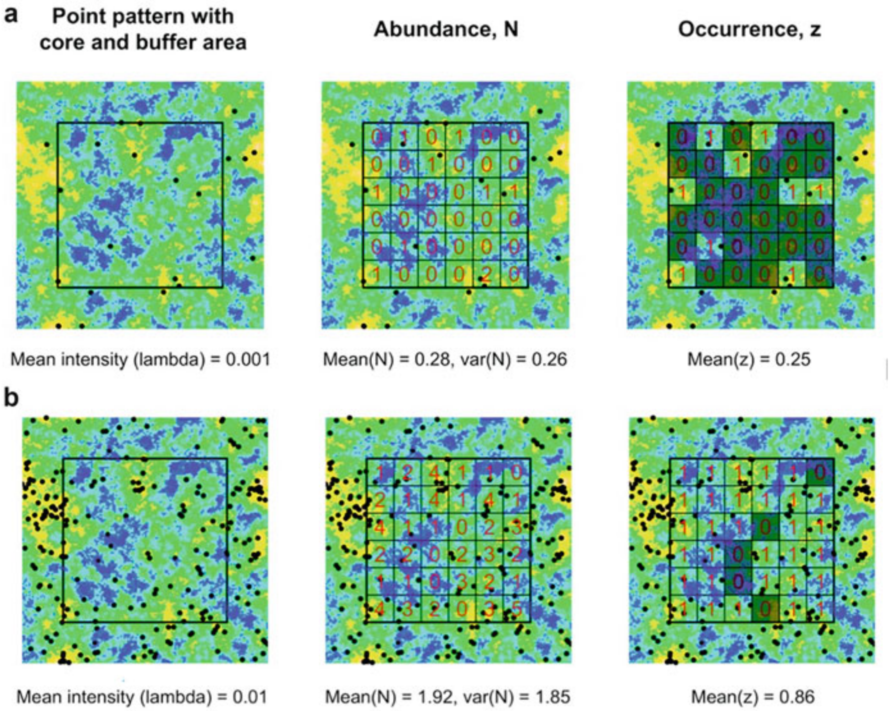

Fig. 1.2 Two examples of the relationships between the point pattern, abundance, and occurrence. The intensity of the lambda parameter is lower in (**a**) than in (**b**). The simulations were produced by the *simPPe* function of the AHM package. (Kéry et al. 2022)

heterogeneity of the habitat, visibility (given by the vegetation cover and the topography of the land), and human activity, among others. (3) *Conditions during samplings (temporal variation)*: time of year, phenology of vegetation, climatic conditions, and time of day are among the most relevant. (4) *Sampling design*: the camera model, sampling effort, distance between sampling units, and the experience of the people who carry out the sampling, among others.

Although in all the methods it is implicitly considered that the expected number of counted animals is itself a function of abundance, at the time of sampling, the detection probability (p) plays an extremely important role and influences the estimate of occupancy, abundance, and density. The higher the abundance, the greater the number of counted animals (n) expected, but this also depends on p. If $p = 1.0$, then the same count would suffice to get an estimate of N. Nonetheless, as usually $p < 1.0$, then an estimate of this detection probability is required. Therefore, it is essential to estimate p to subsequently obtain estimates of the population size. That is, the expected number of animals counted will be a function of the abundance of the population and its probability of detection:

$$E[c] = \hat{p}N$$

Considering that in practice c is an observable quantity and N is a quantity to be estimated, the problem of estimating abundance focuses on estimating p. Thus, a general estimate of N is:

$$\hat{N} = \frac{c}{\hat{p}}$$

That is, the probability of observing different numbers of animals varies depending on the detection probability: as this probability increases, the number of animals observed goes up. An exception occurs in the fixed area methods, where it is assumed that all the individuals within the sampling unit were detected, that is $p = 1.0$. In most of the methods, we do not know what this probability is, and one of the central objectives of the population size estimation is precise to calculate the detection probability. This is done differently depending on the sampling and analysis methods used.

1.4 Aims of This Volume

In this book, we have compiled and discussed reviews and syntheses of the knowledge about the occupancy and abundance of mammals in the Neotropical region. We primarily aim to address these issues at the population level for diverse mammalian taxa in different ecosystems and regions throughout Latin America. The title of this volume consists of three parts: (1) Neotropical Mammals, (2) Occupancy and Abundance, and (3) Hierarchical Analysis. The first has to do with the central ecological parameters on which this book focuses; the second with the taxonomic groups and geographic regions where occupancy and abundance studies were conducted; and the third part refers to the types of statistical procedures applied to analyze these parameters. We hope that this volume will be a reference material for researchers, graduate and undergraduate students, professionals, wildlife managers, environmental authorities, and other persons, groups, organizations, and agencies with an interest in Neotropical mammal research, conservation, and management. These potential users may be attracted to this book because (1) Neotropical mammals are a fascinating group of study and interest for a growing audience worldwide; (2) habitat occupancy and abundance of populations are central parameters for Neotropical mammal conservation and management; and (3) hierarchical models are being widely used to obtain robust estimates and inferences on occupancy and abundance of Neotropical mammals at various scales.

1.5 Book Organization

This volume contains two parts and 15 chapters dealing with different aspects of habitat occupancy, density, and abundance of Neotropical mammal populations. The first part comprises a general introduction (this chapter) and literature reviews on the state of knowledge about those topics for carnivores (Chaps. 2 and 3), primates (Chap. 6), ungulates (Chaps. 5 and 7), and mammalian communities (Chap. 4). The second part of this book consists of case studies where the authors assessed occupancy, distribution, and abundance using hierarchical approaches and building specific models for rodents (Chap. 8), carnivores (Chaps. 9 and 10), primates (Chap. 11), ungulates (Chaps. 12 and 14), and multiple species (Chap. 13) in diverse regions and habitats throughout the Neotropical region. The final Chapter (15) presents an overview of hierarchical methodologies applied to estimate occupancy and abundance.

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Chapter 2
Small Wild Felids of South America: A Review of Studies, Conservation Threats, and Research Needs

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Abstract A total of nine small wild felid species can be found in a diversity of habitats in South America. Hierarchical models (HM) can be used to estimate key population aspects such as their distribution, abundance, density, and the influence of environmental conditions. The HM framework can accommodate errors introduced during the observation process, separating them from the ecological process

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that is key to informing conservation actions. In this chapter, we review studies on small wild felids of South America that estimate abundance, density, and occupancy using HM. We quantify the number of studies per species and ecoregions, as well as assess survey effort, parameter estimates, and their precision. We also qualitatively summarize conservation recommendations arrived at directly from HM results. Based on *a priori* inclusion criteria, we reviewed 81 studies published between 2002 and 2022. The most widely used detection method was camera-trapping. By 2015, occupancy studies had surpassed those of density and abundance in terms of the relative number of publications. The species with the highest number of studies was the ocelot (*Leopardus pardalis*; $n = 49$), and the ones with the least were the Andean cat (*L. jacobita*) and southern tigrina (*L. guttulus*) ($n = 3$ each). *L. pardalis* also dominated HM application in terms of cumulative survey effort (>2 million trap nights). The ocelot showed the broadest range of density estimates and SE values on density and occupancy. The low precision of model estimates but relatively large survey effort for some species suggests the need for more species-specific survey designs (e.g., *H. yagouaroundi* and *L. wiedii*). Conservation recommendations based on the results of HM studies suggest mitigating impacts in three main dimensions: habitat degradation, direct human pressures, and impacts of both native and domestic carnivores. Priority use of HM should be given to species such as *Herpailurus yagouaroundi*, *L. guttulus*, *L. colocolo* complex, and *L. jacobita*, as well as geographical areas for which there are research gaps in demographic parameters.

Keywords Density · Hierarchical models · Felidae · Occupancy · Small wild cats

2.1 Introduction

Except for a few islands and possibly some urban areas, there is no South American terrestrial ecoregion lacking small wild felids. These mammals inhabit the dry Atacama Desert, the Argentinian grasslands, the southern temperate forests, the dry Chaco forests and Caatinga savannas, and the tropical forests of the Amazon basin, among others. Small wild felids can be found almost across the entire altitudinal gradient in the Neotropics, from the coastal areas of the Pacific and Atlantic oceans to the top of Andean mountains at 5000 m above sea level. This

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diversity of habitats is home to nine small wild felids (Macdonald et al. 2010). Most of these belong to the genus *Leopardus*, the ocelot lineage that diverged 8.0 million years ago (Ma), with the exception of the jaguarundi (*Herpailurus yagouaroundi*), which diverged from the puma lineage 6.7 Ma ago (Werdelin et al. 2010).

The distribution of some wild felids across South America can be very broad, spanning several countries and ecoregions (Macdonald et al. 2010). For instance, the pampas cat (*Leopardus colocolo*) – likely a species complex comprising five - spatially-distinct taxonomic units (phylogenetic species; Nascimento et al. 2021) – inhabits mostly open ecosystems, such as the Mediterranean region of Chile, the Andean altiplano, the Argentinian grasslands, coastal deserts, and the Uruguayan and Brazilian savannas. Geoffroy's cat (*L. geoffroyi*) is a widespread species ranging from southern Argentina, Chile, Uruguay, Brazil, Paraguay, and Bolivia, which is associated with forests, shrublands, savannas, and grasslands. The ocelot (*L. pardalis*) inhabits forests and shrublands from North America to Argentina. The recently separated northern (*L. tigrinus*) and southern (*L. guttulus*) tiger cat species (Trigo et al. 2013) are distributed across the Andes and eastern South America, and southern Brazil, respectively. The northern tiger cat is notably absent from the Amazon rainforest types (De Oliveira et al. 2022). The margay (*L. wiedii*) inhabits forests and savannas from North America to southern Uruguay, while the jaguarundi's range covers similar areas but extends further south to central Argentina. Other species have more restricted distributions, such as the güiña (*L. guigna*) within the Mediterranean climate zone of central Chile and temperate forests of the southern cone. Similarly, the Andean cat (*L. jacobita*) occurs across the Andean highlands from Perú to central Chile and Argentina (Marino et al. 2011; Segura-Silva et al. 2021).

Small wild felids and humans interact in diverse ways throughout South America. Some cultures consider them sacred, as is the case with the Andean and pampas cats for indigenous cultures such as the Aymara, Kallawaya, Lickan Antai, and Quechua (Giraldo-Jaramillo 2015). In contrast, other cultures consider them pests and "thieves," owing to the negative impacts they can have on human activities. Several species of small cats, from the larger sized ocelot to the smaller güiña, are often persecuted in retaliation for depredation on poultry and livestock across South America (Gálvez et al. 2021b; Herrmann et al. 2013; Peters et al. 2016). Small wild felids face broader anthropogenic threats, such as habitat loss and fragmentation, diseases from domestic carnivores, and hunting for the wildlife trade (De Oliveira et al. 2020; Inskip and Zimmermann 2009; Macdonald et al. 2010). Despite the diversity and severity of these threats, research on their implications for the status and conservation of small wild felids – both worldwide and in South America – is sorely lacking, particularly when compared with efforts dedicated to larger species of the same family (Brodie 2009).

Key variables related to the conservation and ecology of small felids include their distribution, abundance, density, and the environmental conditions that influence these population attributes. In general, small felids occur at low densities and are difficult to study due to their rarity and elusive behavior (Macdonald and Loveridge 2010). In the last two decades, camera traps have revolutionized our ability to study elusive species, and their use as a survey tool has been steadily increasing (Burton et al. 2015; Wearn and Glover-Kapfer 2017), outperforming many alternative methods (Wearn and Glover-Kapfer 2019). Research with camera traps has focused mainly on carnivores, particularly large species. Since 2008, there has been an increase in the application of complex modeling tools to data obtained from such monitoring programs, often with the aim of estimating the density and/or abundance of naturally marked species, as well as the occupancy of unmarked ones (Burton et al. 2015).

In particular, hierarchical models (HM) are increasingly being used as analytical tools to process wild felid data for different reasons. One of the most important is the fact that HM can accommodate false-negative (and even false-positive) errors during the observation process. Contrary to other measurement errors, like those arising from measuring continuous quantities (e.g., body size, pollutant concentration in the water, and light pollution level), false-negative and false-positive errors do not distribute normally; consequently, cannot be accommodated in the residual of a regression model (Kéry and Royle 2020). False-negative errors are very common during small felid monitoring given their elusiveness and low densities derived from their relatively large home ranges, leading to nondetection in places where they do, in fact, occur. Ignoring false-negative errors can strongly bias monitoring results, with negative consequences on our capacity to infer population parameters and evaluate management and conservation actions (Guillera-Arroita et al. 2014; Lahoz-Monfort et al. 2014).

HM offer the possibility of separating the observation process (by modeling detection probability) from the ecological process (Cressie et al. 2009), which enables researchers to directly estimate both state variables (i.e., distribution, abundance, density, and richness), and rate variables, such as survival probability, birth rate, immigration rate, and death rate, among others. HM can also be used to evaluate associations of environmental conditions with state and/or rate variables, which is key to inform conservation actions. However, applying HM to small wild felids data requires careful design and usually large survey effort due to their low detection probability (Gálvez et al. 2016; Guillera-Arroita 2017; Guillera-Arroita et al. 2010).

In this chapter, we review studies of small wild felids of South America that estimate state variables such as abundance, density, and occupancy using an HM framework. We analyze the distribution of studies and quantify their number per species and ecoregion, as well as describe survey effort, parameter estimates and their precision. For each species, we review the documented threats and conservation recommendations resulting from the application of HM, and propose future survey needs and methodological recommendations. We aim to provide an overview of how HM are being used to study small wild felids across South America, highlighting key research gaps, threats, and conservation implications across the region.

2.2 Methods

Three criteria were used for the inclusion of studies in the present review: (i) the study contained at least one or more of the small felid species known to occur in South America, (ii) the data were analyzed within a hierarchical modeling framework, in which the estimated parameters were associated with abundance, density, occupancy, and/or detection (Kéry and Royle 2020), and (iii) the study was published within the last 20 years (2002–2022). Search engines and repositories were considered using the following order of priority: Web of Science (WoS), Scopus, Google Scholar, SciELO, reference lists of relevant papers identified by expert knowledge, and gray literature in the form of reports from either government, consultancies, or private enterprises. In a first instance, species-specific searches were carried out by independent groups of authors (hereafter, expert groups), each with relevant expertise in the application of HM to a given species. Searches were iterative in nature, as described in Foo et al. (2021), and based on the following common search string structure:

> "*((Common_species_name(s) OR Scientific_name) AND ("hierarchical model*" OR "HM model*" OR occupancy OR abundance OR density OR "N-Mixture" OR capture OR detection OR distribution))*"

Each expert group refined the search and included additional specific terms to improve detection of relevant studies for a given species (Table 2.1). For example, adding the names of geographical locations relevant to each species or the term "co-occurrence" if expert knowledge determined that the species is usually studied as part of a guild rather than on its own. Initial searches were filtered according to our inclusion criteria and duplicates were removed. Multispecies studies were counted once for the purpose of overall descriptive statistics (e.g., location of studies), but counted as one data point for each species for the purpose of analyses carried out at the species level.

For each study included in the final data set, we extracted a series of values and information to conduct our analyses (Table 2.2). We registered formal information about the studies such as author names, title, year of publication, journal, indexing (i.e., WoS, Scopus, and others), number of citations, and link to the paper. Geographic information of where the study was conducted was also recorded, such as country and ecoregion, as well as the name, coordinates, and size of study area. We then documented the characteristics of the HM framework used, including the type of model, marked or unmarked analysis, R package used for the analysis, Bayesian or frequentist approach, and the type of parameters estimated. Additionally, we recorded the type of design used and extracted the number of sampling units, parameter values (together with standard errors), number and type of detection methods, and survey effort. Finally, we summarized the main results, conservation recommendations, and scale of inference.

We described the geographic locations of studies in relation to known species ranges, number of publications per year, country, and ecoregion. For the latter, we used level II ecoregions provided by the U.S. Geological Survey (Omernik and Griffith 2014). To evaluate trends in the popularity and estimation of state variables in the literature, we calculated the percentage of studies within each year that estimated either abundance, density, or occupancy. For each species, we described the types of models used and we identified if publications were either single- or multispecies. In order to evaluate parameter estimates, we created a database with all the estimates (i.e., some studies had several estimates). For this review, we

Table 2.1 Search strings, total results, and number of studies analyzed based on our inclusion criteria of small felid species of South America

Species	Countries where species are known to occur in South America	Common name	Total studies with search string	Studies filtered by inclusion criteria[a]
Leopardus guigna	Chile and Argentina	Güiña, Huiña, kodkod	1886	8
Leopardus jacobita	Chile, Argentina, Peru and Bolivia	Gato andino, Andean Cat	40	3
Leopardus colocolo	Brazil, Peru, Bolivia, Uruguay, Paraguay, Ecuador, Argentina and Chile	Gato colocolo, gato del pajonal, Pampas Cat	2430	6
Leopardus guttulus	Argentina, Brazil, and Paraguay. Possibly Bolivia.	Tirica, Gato-do-mato-pintado, Southern Tiger Cat	164	4
Leopardus tigrinus	Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Peru, Suriname, Venezuela	Tigrillo, Oncilla, Gato-do-mato-pintado, Northern Tiger Cat	1774	12
Leopardus geoffroyi	Argentina, Bolivia, Brazil, Chile, Paraguay, Uruguay	Gato de Geofroy, gato montés, Geoffroy's cat	1374	11
Leopardus wiedii	Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Perú, Suriname, Uruguay, Venezuela	Tigrillo, margay, caucel, gato-peludo, maracajá, Margay	3045	17
Leopardus pardalis	Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Perú, Suriname, Uruguay, Venezuela	Ocelote, jaguatirica, gato-maracajá-verdadeiro, maracajá açu, Ocelot	10,257	74
Herpailurus yagouaroundi	Argentina, Bolivia, Brazil, Colombia, Ecuador, French Guiana, Guyana, Paraguay, Perú, Suriname, Venezuela	Yaguarundi, gato-mourisco, gato-vermelho, Jaguarundi	242	16

[a] Duplicates within each species were filtered. The total of studies for all species includes multispecies studies that are redundant in the filtered lists

interpreted occupancy as the proportion of sites occupied by the species in each survey. In the case of density, we used estimates that had ½ MMDM (mean maximum distance moved) values in the capture–recapture framework and standardized the estimates to individuals per 100 km^2. To describe the dispersion of parameter estimates and their precision, we plotted the predicted occupancy, detection, and density estimates against their reported standard error. Horizontal dispersion in such plots represents the range of estimates for a particular species, while vertical dispersion represents variation in the precision of estimates. We only evaluated density estimates and excluded abundance because the former could be easily compared among studies. To describe the survey effort per species, we plotted

Table 2.2 Five domains of information that were collected from each study that complied with the inclusion criteria

Domain	Data collected
Formal information	(1) Publication information such as authors, title, year, journal, link; (2) number of citations; (3) key words; (4) type of article (i.e., journal article, report, among others).
Geographic information	(1) Country where study was carried out; (2) location of study area(s); (3) size of study area; (4) ecoregion; (5) if study areas were within a protected area
Hierarchical models	(1) Type of model such as occupancy, capture–recapture; (2) marked or unmarked analysis; (3) statistical package or program used; (4) Bayesian or frequentist; (5) type of parameter estimated (e.g., Ψ, p)
Design and quantitative results	(1) Values of parameter estimate and reported standard error; (2) number of sample units; (3) type and number of detection methods per sample unit; (4) total survey effort; (5) days considered a sampling occasion; (6) number of sampling occasions.
Conservation implications	(1) Summary of main results; (2) conservation recommendations proposed; (3) scale of inference.

cumulative camera-trapping effort and the number of spatial sample units of each study. Additionally, and to evaluate precision of parameter estimates, we plotted the ratio between the standard error (SE) and the estimate (i.e., SE/estimate) for both density and occupancy. Finally, we summarized conservation recommendations that were directly associated with results of publications that used HM to estimate parameters and that evaluated species–environment relationships (e.g., identification of key habitats or landscapes, or relevance of species interactions).

2.3 Results

Initial searches using species-specific strings across the range of search engines considered yielded a total of 21,212 records. Based on our inclusion criteria, these were filtered down to 151 records (Table 2.1). The latter, however, included records originating from the same study (in the case of multispecies studies). Removing such duplicates resulted in a total number of 81 studies published between 2002 and 2022. The main search engines that provided unique results (i.e., corrected for multispecies studies) were WoS ($n = 42$) and Google Scholar ($n = 36$), followed by reference lists and expert knowledge ($n = 2$), and Scopus ($n = 1$). Records consisted primarily of scientific papers ($n = 71$), followed by theses and reports ($n = 9$). Most studies were conducted exclusively within protected areas ($n = 40$), followed by surveys carried out exclusively outside of them ($n = 26$). A smaller subset of studies considered both protected and unprotected areas in their surveys ($n = 18$). All nine species had been the target of at least one study employing an HM framework (Fig. 2.1), with a high representation for the ocelot (*L. pardalis*; $n = 49$ studies) and a comparatively smaller one for species such as the southern tiger cat (*L. guttulus*; $n = 3$) and the Andean cat (*L. jacobita*; $n = 3$).

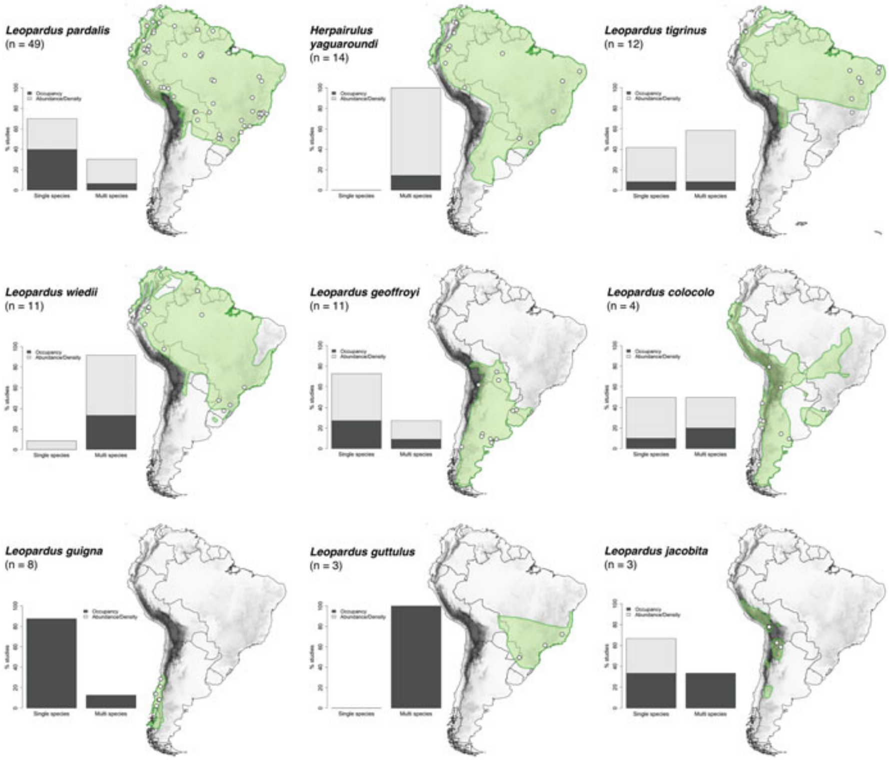

Fig. 2.1 Range of the nine small cats of South America from the IUCN Red list (green polygon), geographic distribution of hierarchical model studies for each species included in this study (white dots) and counts of studies (graphs lower left) that describe the number of density-abundance (dark gray color in bar) and occupancy studies (light gray color in bar) as well as single species versus multiple species studies. Because of the latter some dots may be the same for several species

The most widely used method of detection was camera traps ($n = 81$), with a small number of studies using telemetry, scats, tracks, and hair-trap surveys to complement photographic records. From 2015, studies per year increased in number and occupancy models gained popularity (i.e., >70% by 2022) and surpassed studies focused on estimating density and abundance (Fig. 2.2a, b). The country with the most studies was Brazil, and the ecoregion with most studies was the Atlantic Forest (Fig. 2.2c, d). The least represented ecoregion was the Fuegian fiords and forests (Fig. 2.2d). More than half of studies ($n = 46$) used some type of occupancy model (e.g., conditional two species or multiseason among others; see database repository for more details: https://repositorio.uc.cl/handle/11534/66873) and unmarked framework (i.e., not identifying individuals). The remainder of models ($n = 35$) used some variation of capture–recapture analysis, such as spatially explicit capture–recapture (SCR), employing individual-level capture histories from naturally marked species (e.g., *L. jacobita* and *L. pardalis*). Only one study used unmarked models such as

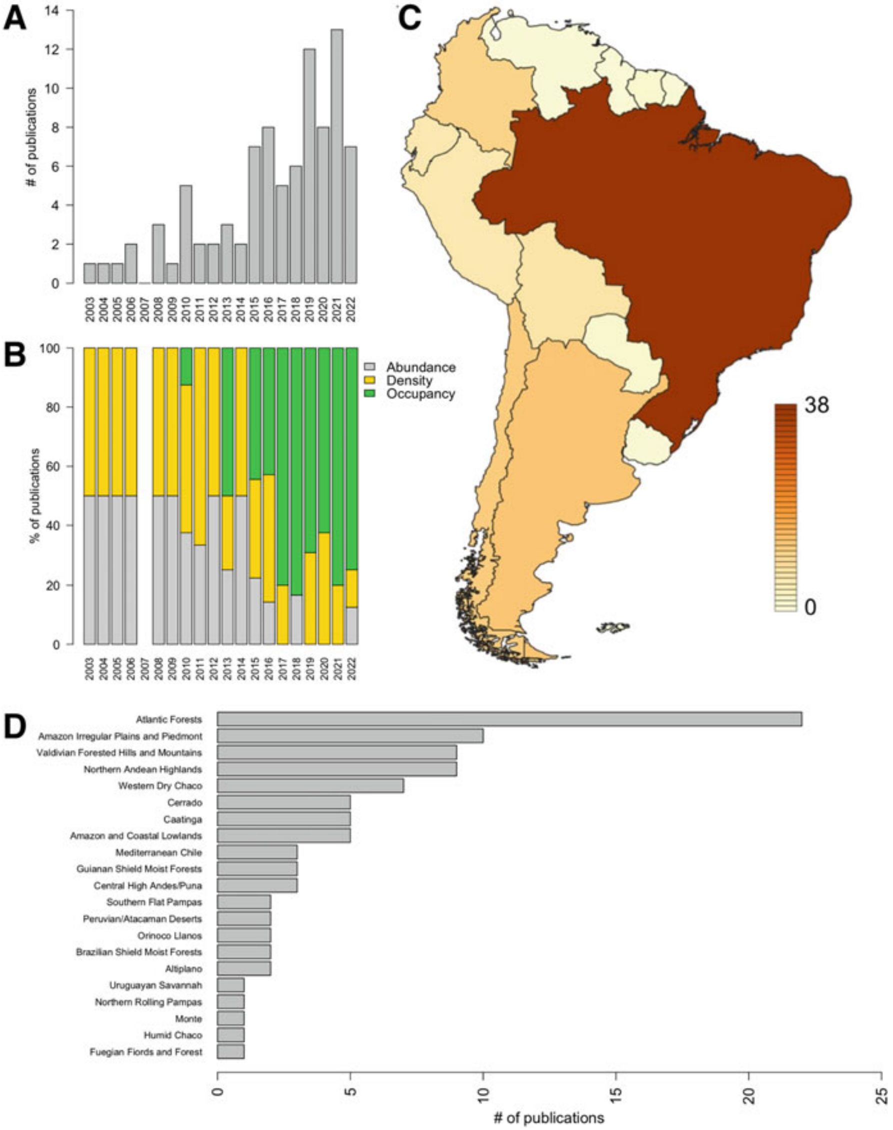

Fig. 2.2 Summary of publications that met our inclusion criteria in terms of number of publications per year (**a**), per year stacked percentage of density, abundance, and occupancy publications (**b**), number of publications per country (**c**), and number of publications per level II ecoregion provided by the U.S. Geological Survey (**d**)

N-mixture to estimate abundance. Notably, 70% of the analyses of marked species estimated the abundance and/or density of the ocelot (*L. pardalis*), while species such as the güiña (*L. guigna*) have only been studied with unmarked analyses, particularly occupancy models (Fig. 2.1). Most studies were focused on a single

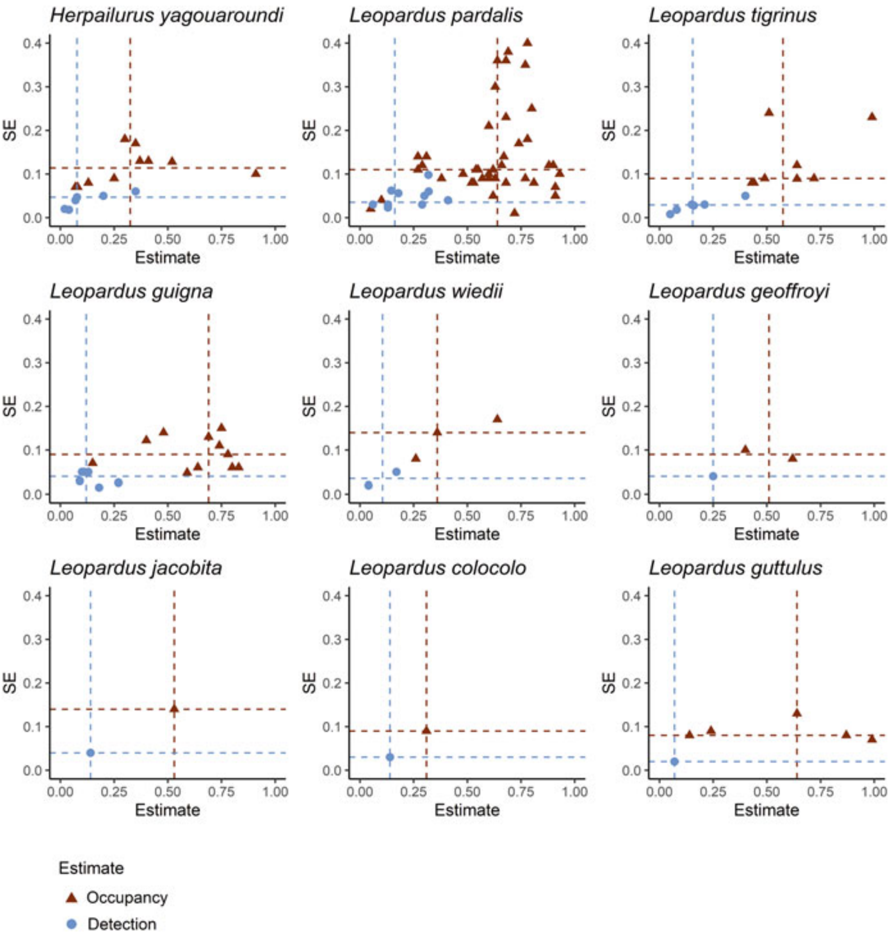

Fig. 2.3 Occupancy and detection probability estimates and their respective standard error (SE) of South American small wild cats using hierarchical models. Dots represent study cases, whereas dashed lines represent the median of parameters for each species. Cases where standard error was not reported are not shown

species ($n = 56$) while the rest targeted multiple species ($n = 25$), most of which were studies of tropical cats ($n = 22$). Additionally, species such as the northern and southern tiger cats (*L. tigrinus, L. guttulus*), the margay (*L. wiedii*), and the jaguarundi (*H. yagouaroundi*) were primarily included in multispecies studies (Fig. 2.1).

L. pardalis is also the species with more occupancy estimations (52), while others have as few as one estimation, as is the case of *L. jacobita* (Fig. 2.3). The species with the lowest estimates of occupancy probability (i.e., proportion of sites occupied) were *L. guttulus* (0.02), *L. pardalis* (0.05), and *H. yagouaroundi* (0.07). At the same time, *L. guttulus* showed a very high dispersion of estimates, even having the highest occupancy estimates together with *L. tigrinus*, with some estimates reaching

Table 2.3 Summary statistics for occupancy, detection probability, and density (ind./100 km^2) of each small wild felid

Species	Occupancy median (sd)	Det. prob. median (sd)	Density median (sd)	Occupancy range	Det. prob. range	Density range
H. yagouaroundi	0.34 (0.22)	0.02 (0.09)	7.53 (4.18)	0.07–0.91	0.001–0.35	3.28–13.06
L. colocolo	0.31	0.14	11.34 (37.04)	0.31–0.31	0.14–0.14	5.31–78
L. geoffroyi	0.41 (0.2)	0.25 (0.3)	16.21 (16.89)	0.4–0.85	0.15–0.88	1–41.78
L. guigna	0.66 (0.2)	0.19 (0.06)	–	0.15–0.83	0.09–0.27	–
L. guttulus	0.12 (0.35)	0.07	–	0.02–0.99	0.07–0.07	–
L. jacobita	0.53	0.14	6.96 (2.62)	0.53–0.53	0.14–0.14	6.45–12
L. pardalis	0.64 (0.21)	0.08 (0.11)	16.2 (19.99)	0.05–0.93	0.004–0.41	1.8–94.7
L. tigrinus	0.58 (0.17)	0.16 (0.12)	5.97 (4.24)	0.43–0.99	0.01–0.4	2.54–11.3
L. wiedii	0.58 (0.19)	0.02 (0.05)	12.57 (10.34)	0.24–0.67	0.001–0.17	9.6–37.4

We show median and standard deviation (in parenthesis) of estimates and ranges for each parameter. When there is one estimate, standard deviation is not calculated

nearly 100% of occupancy. *L. pardalis* also showed high values of occupancy and the highest variation in the SE. *H. yagouaroundi* and *L. guttulus* had the lowest median probability of detection (0.02 and 0.07, respectively), while *L. geoffroyi* had the highest (0.25), as shown in Table 2.3. For all species, the SE associated with detection probability was similar.

As with occupancy estimates, *L. pardalis* presented the highest number of density estimations (79, Fig. 2.4) with a high dispersion of estimates (i.e., low and high densities). Furthermore, *L. pardalis* reached the highest estimation of density between all species (94.7 ind./100 km^2), followed by *L. colocolo* (78 ind./100 km^2), *L. geoffroyi* (41.78 ind./100 km^2), and *L. wiedii* (37.4 ind./100 km^2). Except for *L. colocolo*, these species presented the highest values for estimate SEs. Among the species with the lowest density estimations were *L. geoffroyi* (1 ind./100 km^2), *L. pardalis* (1.8 ind./100 km^2), and *H. yagouaroundi* (3.28 ind./100 km^2) (Table 2.3, Fig. 2.4). A summary of median values and ranges for density, occupancy, and detection of each species is shown in Table 2.3.

Survey effort per species, measured as both the cumulative number of camera trap days and the number of sample units, showed a very strong bias toward *L. pardalis,* with a nearly tenfold difference respect to the next species with higher survey effort, *H. yagouaroundi* (Fig. 2.5a). Apart from some outliers, studies ranged from less than 10 to as many as 200 sampling units (Fig. 2.5b). Species such as *L. geoffroyi*, *L. colocolo*, and *L. jacobita* showed the lowest number of sampling units per

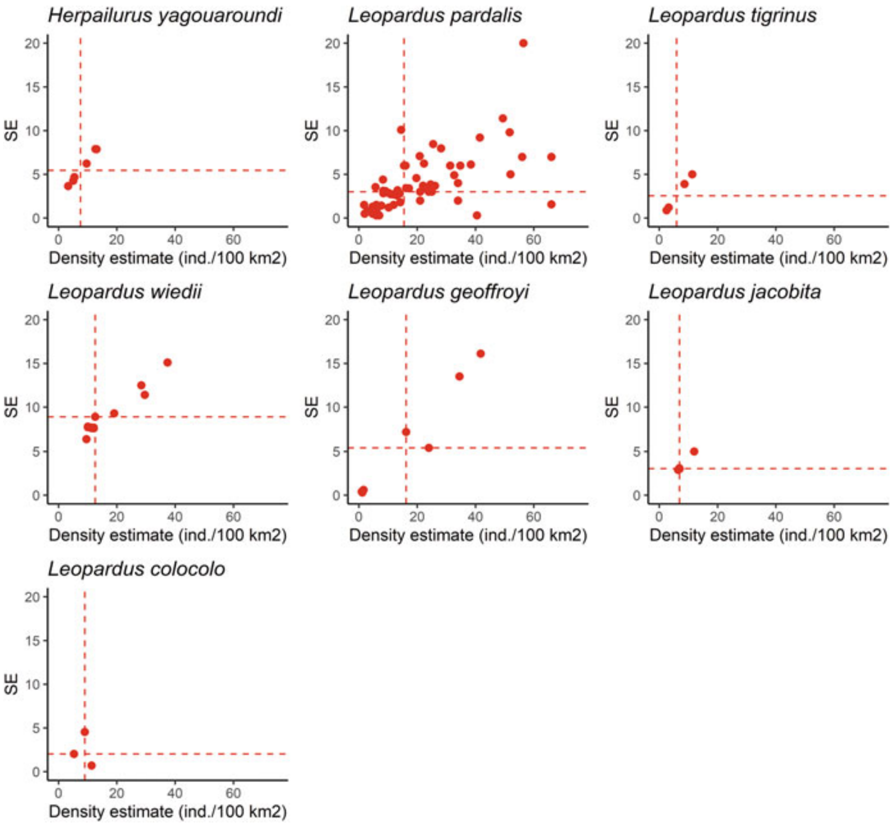

Fig. 2.4 Density estimates and their respective standard error (SE) of South American small wild cats using hierarchical models. Dots represent study cases, whereas dashed lines represent the median of parameters for each species. Cases where standard error was not reported are not shown

study. In terms of model estimate precision (Fig. 2.5c, d), *L. pardalis* showed the highest precision of density estimates (i.e., low SE/estimate ratio) compared to species such as *H. yagouaroundi* and *L. wiedii* with median ratio values over 0.6. For precision of occupancy model estimates, *L. pardalis* showed higher dispersion but the median was similar to *L. tigrinus*, *L. guigna*, *L. guttulus,* and *L. geoffroyi*. Again, *H. yagouaroundi* and *L. wiedii* had the lowest occupancy estimate precision, but the former exhibited high dispersion of values. Species such as *L. colocolo* and *L jacobita* also showed relatively low precision of estimates, but the information was based on very few data points.

Conservation recommendations originating from HM study results for each species are summarized in Table 2.4. These can be grouped into three main recommendation categories: (i) those highlighting the important habitat/landscape configurations requiring protection and ways this may be achieved; (ii) those associated with human activities that negatively impact the species and proposals to mitigate

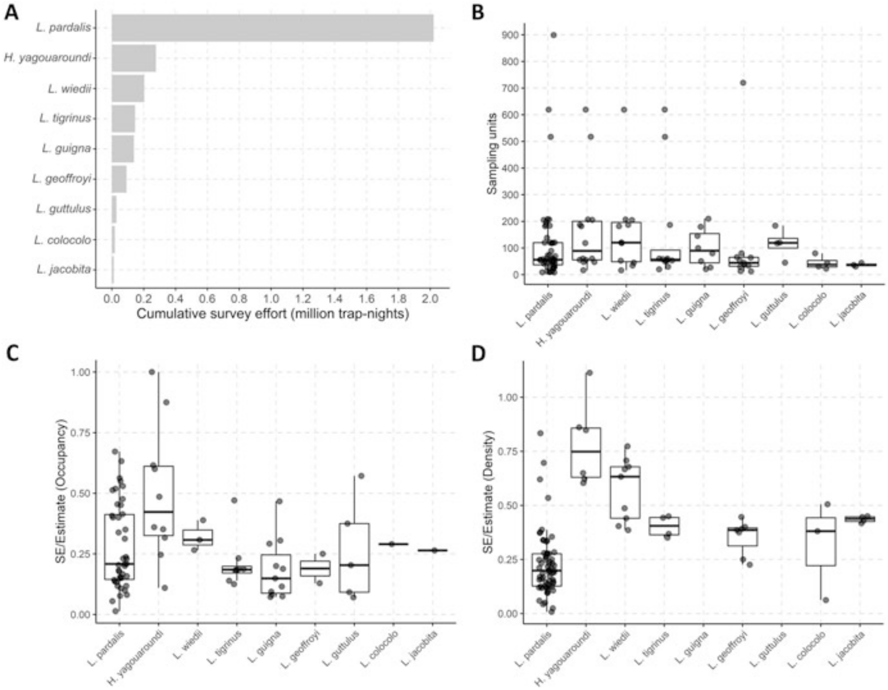

Fig. 2.5 Summary of survey and sampling effort and estimate precision of HM for small wild felids of South America. Panels show (**a**) the accumulation of camera-trap survey nights considering all the studies for each species; (**b**) the number of spatial sampling units for each study; and both (**c**) and (**d**) show the ratio between the standard error (SE) and the estimate (i.e., SE/estimate) for occupancy and density, respectively, as a measure of parameter estimate precision. Higher values indicate low precision of parameter estimates. Lines in boxplots represent median values

those activities; and (iii) those focused on managing the impacts of interspecific interactions with other native or domestic carnivores.

2.4 Discussion

Compared to small species, large carnivores have historically received more attention and research funding worldwide (Brodie 2009; Brooke et al. 2014). South America is no exception to this pattern. Hierarchical models have been used to study all the small cats in South America but with an unbalanced focus on larger species such as *L. pardalis* and ecoregions such as the Atlantic Forest. The reasons for this bias are likely varied, but probably include funding availability, distribution of researchers and or universities, density of felids in the study area, geographic

Table 2.4 Summary of conservation recommendations and discussions in research conducted with hierarchical models of South American small wild cats

Species	Conservation recommendations
Leopardus guigna	Güiñas can tolerate some degree of habitat loss and can survive in agricultural landscapes. Safeguarding fragments and remnant native vegetation and their quality (e.g., understory vegetation density) as habitats will be key. Restoration of riparian areas and forest fragments is necessary. Land subdivision from encroachment of urban centers toward rural areas is an increasing threat.
Leopardus jacobita	Human–wildlife conflict and mining activity (at different spatial scales) are emergent drivers of Andean cat survival in the Altiplano region. In addition, maintaining prey density and legal protection of suitable habitats can have very important ecological implications for population connectivity. Thus, the long-term persistence of high quality (in terms of prey availability) and connected habitats may ensure a landscape-level viability of the species.
Leopardus colocolo	Pampas cat is apparently tolerant to degraded habitats as it can live in human-dominated landscapes, which may be affected by overgrazing or agricultural activity, using remnants of native forests and scrublands. It is also suspected that the poor management of domestic cats and dogs in the pampas cat habitat modifies the behavior of the species, affecting its survival. In addition, the low densities of the species may prevent a better understanding of its ecology and potential threats.
Leopardus guttulus	Both in Brazil and in Argentina, *Leopardus guttulus* is more abundant in forest dominated landscapes where ocelots are absent or not abundant. This may arise from the strong competitive/predator effect exerted by the ocelot. Thus, *L. guttulus* tends to be more frequently found outside protected areas, where forested areas intermingle with environments with some level of human intervention and productive activities. Therefore, for this species, ensuring the long-term maintenance of connectivity of forest fragments in private lands is highly important.
Leopardus tigrinus	Tiger cats have been documented to be associated to well-preserved native covers and to be sensitive to human activities including invasive species like dogs. It is necessary to reinforce and expand the current network of protected areas as well as to involve private stakeholders to improve the connectivity of tiger cats across degraded landscapes. In addition, environmental education, technical assistance for poultry management and recurrent inspections by environmental agencies may benefit tiger cat populations in proximity to agrarian settlements.
Leopardus geoffroyi	Geoffroy's cat displays a certain level of tolerance toward the alterations in its habitat caused by livestock management and agricultural practices. The long-term survival of the species is primarily contingent upon the preservation of these natural ecosystems. To safeguard the viability and persistence of the species populations within their geographic range, it is recommended to prioritize the conservation and restoration of their natural habitats, which comprise the mosaic of xeric forests and grasslands, forest patches, and riparian forests.
Leopardus wiedii	The documented conservation recommendations for margays include control of feral pigs, implementation of environmental education campaigns, and law enforcement to reduce poaching pressures. As a forest-dwelling felid, active management practices directed toward the regeneration of small forest fragments are thought to induce a positive response in

(continued)

Table 2.4 (continued)

Species	Conservation recommendations
	its population densities. Understanding the impact of dam construction on margay populations is also encouraged. This is particularly important when planning to construct water reservoirs while improving landscape connectivity or to reject unfavorable designs through evidence-based arguments. In addition, strengthening country-wide transboundary conservation policies toward large tracts of Amazon rainforests that are shielded by indigenous communities and national parks between Colombia, Peru, and Ecuador resulted in a strong benefit for margay populations in the region**.**
Leopardus pardalis	Strengthening land-use planning to encourage the protection of existing native habitats across productive landscapes and reduce poaching pressures were conservation recommendations frequently mentioned for ocelots. Maintaining and improving the connectivity among vital biological corridors for the species between their Central (Mesoamerican Biological Corridor) and South American (Green Corridor of Misiones) populations was also suggested. Implementing incentive-based approaches such as tax breaks, subsidized credits, and premium prices for certified agricultural products to increase the involvement of stakeholders into the conservation planning was also recommended. Avoiding the removal of the emergent understory vegetation in oil palm plantations and mitigation of seismic lines (i.e., gas and oil exploration) may improve the permeability of the landscape matrix for this felid. Other conservation recommendations included canine vaccination and neutering campaigns.
Herpailurus yagouaroundi	Jaguarundis are documented to be more resilient than other small felids in terms of their ability to occupy degraded landscapes such as oil palm plantations in as much as minimal undergrowth vegetation therein is granted. Thus, considering the preservation of the structural complexity in the microhabitats across agricultural practices is recommended to sustain the prey base of jaguarundis. Other recommendations include incentive-based actions to make landowners more receptive to joining efforts for banning hunting and logging in their lands. It is likely that providing technical assistance to avoid jaguarundi mortality induced by retaliation due to poultry depredation would also provide benefits for the species. Another recommendation to support the persistence of jaguarundis in arid landscapes like the Caatinga, is the installation of artificial water troughs, as this resource is scarce almost all year round. It is also important to control and track the impacts that invasive species such as wild pigs and dogs could have on the ecological resilience of jaguarundis in a context of landscape degradation. Finally, as with other small felids, the creation of new protected areas and the strengthening of the already existing ones are recurrent conservation actions that are suggested to strongly benefit jaguarundi populations.

accessibility, and ecological traits of the study species. For many species, studies only originate from a small area within the species' estimated range. This could be an indication that, for most species, we have limited knowledge on their population dynamics, vital rates, and habitat associations across their distribution.

Additionally, the high dispersion of estimates and their precision for many species could be indicative of suboptimal sampling (Guillera-Arroita et al. 2010) and/or the nonspecies-specific nature of survey designs (Gálvez et al. 2016). This could be the case for *H. yagouaroundi* and *L. wiedii*, which despite showing relatively high survey effort compared to other species, were primarily studied as part of multispecies surveys in which they were most likely not the target species. In contrast, species such as *L. guigna,* with similar levels of cumulative camera trap days and number of sampling units, but associated with estimates obtained from species-specific designs (e.g., Fleschutz et al. 2016; e.g., Gálvez et al. 2018), showed lower dispersion of estimates and better model estimate precision.

It is uncertain if results regarding parameter precision reflect survey design/effort or estimates reflect differences in population and ecological conditions of different study areas. In both density and occupancy studies, species-specific study designs are warranted for more accurate and precise estimates. When the focus is to study multiple species, we recommend planning survey design and effort (e.g., number of sampling units and sampling occasions) considering as much as possible the full range of target species, be them common or rare. Simulations to determine sample sizes can be performed using reference levels of occupancy, detection and density reported and compiled in this chapter (Table 2.3).

Evaluating the relationship between occupancy estimates and abundance/density can provide valuable insights into species ecology (Gaston et al. 2000; Linden et al. 2017; Steenweg et al. 2018). Individual recognition for density studies is challenging, even when setting up two cameras (De Oliveira, pers. comm). This is particularly the case for species with inconspicuous fur patterns (e.g., *H. yagouaroundi* and *L. colocolo*), which is possibly the reason why occupancy studies have significantly increased in recent years. Priority should be given to the evaluation of the relationship between occupancy estimates and abundance/density for each species assuming the former is logistically easier to apply given that only one detection device may be used and there is no need for individual recognition.

Population status and specific conservation recommendations are needed for the long-term persistence of carnivores in general (Karanth and Chellam 2009). Undoubtedly, there is uncertainty regarding the population status of small wild cats and guidelines for habitat and landscape conservation actions derived from HM results. Nonetheless, most studies included in this review have evaluated necessary aspects of landscape, habitat and/or anthropogenic pressures on all small wild cats and provide some guidance with respect to conservation (i.e., notwithstanding the need to address the human dimension). We provide a further discussion for each species.

2.4.1 Herpailurus yagouaroundi

The jaguarundi has the broadest geographical distribution of all South American felids. Nevertheless, we did not find a single study specifically focused on jaguarundi abundance or occupancy, with available data only originating from multispecies studies that included this species. Data from these multispecies assessments suggest jaguarundis are very flexible, with the species recorded in palm oil plantations in Colombia (Pardo et al. 2019) and areas near human settlements in the Brazilian Caatinga (Fox-Rosales and De Oliveira 2022). Some of the least precise occupancy, detectability, and density estimates for South American small felids are from jaguarundis (Fig. 2.4). This could be due to the species' inherent low abundance throughout its range, confounded with suboptimal sampling because most surveys are designed to target other sympatric species. Furthermore, there is a lack of HM studies for this species within several ecoregions in which it is known to occur such as the Cerrado, the Llanos, or Chaco. We recommend surveys specifically targeting jaguarundis to obtain more precise estimates of abundance and occupancy. Another research interest for this species would be evaluating spatial co-occurrence with other felids, such as Pampas (*L. colocolo*) and Geoffroy's cats (*L. geoffroyi*) in the southernmost parts of its range, and with ocelot, margay, and both northern and southern tiger cats in the northern and central parts of its distribution.

2.4.2 Leopardus geoffroyi

The detection probability values and the comparison of precision-estimating models in relation to survey effort for Geoffroy's cat suggest that it is not difficult to collect data for this species. In addition, together with *L. pardalis* and *L. wiedii*, *L. geoffroyi* presented the highest median density among the species included in this review (Fig. 2.4, Table 2.3). The results of our work seem to agree with the suggestion that Geoffroy's cat is relatively common (Pereira et al. 2014). However, it is also important to consider that there are only two studies estimating density for this species using SCR models, one in Brazil (Tirelli et al. 2019) and the other in Argentina (Caruso et al. 2012). The species' occupancy probability was estimated in seven studies across Argentina, Uruguay, Brazil, and Paraguay (Cameroni 2008; Gantchoff and Belant 2016; Caruso et al. 2020; Weiler et al. 2020; Turcatti 2021; Martínez et al. 2022). Furthermore, although the species shows high density values in some areas, this pattern cannot necessarily be generalized at larger spatial scales. Lastly, a better understanding of the main threats facing the species, as well as estimates of mortality, dispersal, and hybridization rates (with the southern tiger cat *L. guttulus*; Trigo et al. 2013; Sartor et al. 2021) will be crucial to reliably assessing the spatial structure and dynamics of populations in response to conservation decisions.

2.4.3 Leopardus guttulus

The southern tiger cat is a globally threatened species (De Oliveira et al. 2014) inhabiting the Atlantic Forest, which is one of the most threatened ecoregions in South America. This is one of the least studied small Neotropical felids, with only four multispecies studies using HM to estimate population parameters. There are no density estimates for this species so far. This scarcity of studies could be the result, at least in part, of the recent splitting from its sister species, *L. tigrinus*, a relatively more studied felid, and because of its reduced distribution range, although studies are lacking to define its current limits. Density values for *L. tigrinus* are small when compared to other South American cats, but these cannot be extrapolated to the *L. guttulus* due to the range difference and likely lower densities and population sizes (e.g., see, Di Bitetti et al. 2008 for a latitudinal effect on the density of a Neotropical cat). Thus, population and density estimates are sorely needed for the southern tiger cat.

The Southern tiger cat has been studied using HM at only three Atlantic Forest locations. These studies have estimated the detection probability (p) and site occupancy or use (ψ) by *L. guttulus*, producing estimates that reveal wide variation among sites, apparently larger than that of other South American cats (see Fig. 2.3). This species has a higher probability of habitat use (and seems to be more abundant) in areas with lower probability of ocelot occupancy, usually areas with relatively lower protection and higher human intervention and forest fragmentation (Cruz et al. 2018; Di Bitetti et al. 2010; and see also Nagy-Reis et al. 2017). This may result from intraguild competition with the larger ocelot (Cruz et al. 2018; De Oliveira and Pereira 2014) and may explain the high variation in occupancy across sites shown by the southern tiger cat. Thus, this little cat seems to represent a challenge in terms of defining conservation objectives for South American felids, since there seems to be a trade-off between preserving and restoring its best habitat conditions and preserving suitable habitat for the ocelot and other larger felid species.

2.4.4 Leopardus tigrinus

Despite a range spanning over ten South American countries, all studies on the globally threatened northern tiger cat (Payán and De Oliveira 2016) included in our database were conducted either in Colombia or Brazil. Density estimates for this species were considerably lower compared to those for ocelot and Geoffroy's cat (Fig. 2.4) and were conducted predominantly in the Caatinga and Cerrado domains of northeast Brazil. Occupancy studies suggest the species tends to avoid areas near human settlements in the Cerrado savannas, the semiarid Caatinga and in the cloud forests of the Colombian Andes. Northern tiger cat occupancy and detectability was negatively impacted by ocelot numbers and occupancy in areas of the dry Caatinga and Cerrado savannas (Dias et al. 2019; Oliveira 2018). In the latter habitats, the species is associated with dense vegetation formations (Fox-Rosales and De Oliveira 2022; Lima 2020; Marinho et al. 2018). In the cloud forests of the Colombian Andes, northern tiger cats were mainly associated with well-preserved forests, used areas with high microhabitat structural complexity, and with high prey availability (Cepeda-Duque 2022). As in the lowland Cerrado and Caatinga, tiger cats in the mountain cloud forests are likely to benefit from the involvement of landowners and communities in conservation initiatives to preserve native forest cover and improve the connectivity of populations in degraded landscapes (Bedoya-Durán et al. 2021;

De Oliveira et al. 2020; Fox-Rosales and De Oliveira 2022). Based on our review, we highlight the need for further studies of northern tiger cats across its other range countries. Further information on northern tiger cat habitat use preferences and density estimates are urgently needed.

2.4.5 Leopardus guigna

Occupancy models are the only HM that have been applied to study *L. guigna*. Occupancy estimates have been quite consistent throughout the range and studies, most likely due to the fact that surveys have been conducted mainly within the Valdivian forested hills and mountains ecoregion, using species-specific sampling designs (Fleschutz et al. 2016; Gálvez et al. 2016, 2018, 2021a). We only found one study in the Mediterranean Chile ecoregion revealing the importance of mountain ravines within remnant native vegetation surrounding agricultural land, which also showed sympatry with *L. colocolo* (Beltrami et al. 2023). The lack of studies in this densely populated ecoregion (i.e., nearly half of the population of Chile lives in this area) suggests an urgent need to further understand the species' population status and the impacts of human pressure (e.g., forest fires, land clearing for agriculture, and domestic pets). In the southern ecoregion, analyses with HM have highlighted the need to influence public policy regarding land-use change, particularly in the conversion of agricultural land to residential areas and domestic carnivore management (Gálvez et al. 2018, 2021a). In particular, one study took a socioecological approach and included social variables within dynamic occupancy models (Gálvez et al. 2018), which is not common according to our review. We do not know the relationship between occupancy probability and density/abundance of *L guigna*. It is our view that this information would be highly beneficial given that occupancy studies have been conducted systematically in some areas. Novel ways and methods to provide individual recognition from camera traps or other methods would be highly valuable for this purpose and to improve population estimates of this species. Finally, there is a complete absence of studies in Argentina, which are thoroughly needed.

2.4.6 Leopardus jacobita

The Andean cat is one of the world's most elusive and rare small wildcats, translating into low HM detection probabilities (e.g., Lucherini et al. 2008). Increasing detectability, however, is crucial when estimates of abundance and/or distribution are required to develop conservation strategies, particularly for the Americas' most threatened felid. One of the causes of the rarity of the Andean cat is that most records of the species are concentrated in the high Andes above 3600 m in Argentina, Bolivia, Chile, and Peru. Recent systematic surveys along with anecdotal records have detected the species at lower elevations in the southern Andes of Argentina (Tellaeche et al. 2020) and in central Chile (Segura-Silva et al. 2021; Villalobos et al. 2022). As a result, its distribution range has extended to the south and outside the Andes, into Mediterranean, semiarid, and Patagonian steppe habitats at elevations as low as 650 m.

To date, few studies on this species have reported demographic parameters including density estimates based on the detection of different individuals using two cameras per station. Estimates based on systematic camera-trapping and HM resulted in a mean detection probability of 0.07 and a density of 7–12 Andean cats per 100 km^2 in northwestern Argentina (Reppucci et al. 2011). Using a classical closed-population model with constant detection probabilities, a preliminary estimate of 1.8 Andean cats per 100 km^2 was calculated in central western Bolivia (Huaranca et al. 2019). A more recent study conducted in the same area but using spatially explicit capture–recapture (SECR) framework with variable detection function estimated a cat density between 6.5 and 6.1 animals per 100 km^2 (Huaranca et al. 2022), which is closer to the values reported by Reppucci et al. (2011). On the other hand, an analysis of Andean cat occupancy associates a low probability of habitat use with an increase in the number of camelid livestock such as llamas (*Lama glama*) and alpacas (*Vicugna pacos*), which graze in the habitat of the Andean cat, and modify its behavior. This modification may be due to an increase in the perception of risk or a decrease in habitat quality for its main prey, the mountain vizcacha *Lagidium viscacia* (Huaranca et al. 2022). Thus, although large differences in density estimation found between studies may be due to sampling effort, we strongly argue that the use of a more robust method that accounts for imperfect detection/capture will provide more unbiased estimates of demographic parameters such as density and occupancy. Given its conservation status and the limited knowledge on the species, applying HM is urgent for evaluating Andean cat populations and their ecological drivers. The newly discovered extension of its range close to human settlements should be a priority given relevant questions that may be assessed regarding the influence of human pressure and habitat quality for the long-term persistence of the Andean cat.

2.4.7 Leopardus pardalis

As the dominant mesopredator of the Neotropical realm, the ocelot is by far the most studied small felid in South America (De Oliveira et al. 2010, 2022). Numerous hierarchical modeling studies of this predator have been conducted, either using camera traps alone (Bolze et al. 2021; Massara et al. 2018, 2015; Wang et al. 2019) or complementary survey methods (Dillon and Kelly 2008; Maffei and Noss 2008; Rodgers et al. 2014). These have both directly (Boron et al. 2020; García-R et al. 2019) and indirectly focused on this felid (Cruz et al. 2018; Maffei et al. 2005; Meyer et al. 2020). Most of the hierarchical modeling research on ocelots has been conducted in the Atlantic Forest, a highly threatened biodiversity hotspot in which the research interest is often focused on understanding how ocelots respond to anthropogenic disturbance (Massara et al. 2015; Cruz et al. 2018). Mesopredator release of ocelots in the face of decreasing jaguar and puma populations has been suggested as a plausible explanation of why ocelots are increasing in the Atlantic Forest (Massara et al. 2015). In Barro Colorado Island for instance, ocelot densities reach up to 1.59 ind./km^2, the highest density estimate ever reported for the species, in a region where jaguars have been extirpated (Moreno et al. 2006). However, whereas some studies failed to find a correlation between either jaguar or puma densities and that of the ocelot (De Oliveira et al. 2010, 2021), others have shown a positive correlation between the relative abundance of ocelots and that of jaguars and pumas at a landscape-regional level (Di Bitetti et al. 2010). On the other hand, some studies in this review found that coexistence between ocelots and the remnant populations of larger felids in well-preserved areas would also be possible through resource partitioning (Di Bitetti et al. 2006; Massara et al. 2015). In contrast, several other ecosystems such as northern Andes, Dry Chaco, Amazon, Cerrado, Caatinga, and the Guyana Shield still present important knowledge gaps for the species (García-R et al. 2019; Wang et al. 2019).

The density of ocelots is highly variable among the different habitat types of South America (De la Torre et al. 2016; De Oliveira et al. 2010), and it is tentative to conjecture that some macroecological processes are governing the widespread occurrence of this predator in the continent (Di Bitetti et al. 2008; but see Kasper et al. 2015; da Rocha et al. 2016). Recent modeling has shown that forest cover and temperature are the most important variables influencing ocelot density (De Oliveira et al. 2022). Large variations in species densities are expected to occur, as favorable conditions (including the prey base) vary among sites. Nevertheless, there is also a great deal of variation depending on the model used. With nonspatial capture–recapture models, densities tend to be overestimated and data available ranged from 0.94 ind./km^2 in the Western Amazon (Kolowski and Alonso 2010) to 0.02 ind./km^2 in the Southern Atlantic Forest (Massara et al. 2015). In contrast, density estimates from spatial capture–recapture models tended to be more conservative, ranging from 0.51 ind./km^2 in the Chaco Dry Forest (Noss et al. 2012) to 0.16 ind./km^2 in Central Guyana (Roopsind et al. 2017) and 0.11 ind./km^2 in the Middle Magdalena Inter-Andean Valley of Colombia (Boron et al. 2022). It has been shown that ocelot densities negatively impact those of the other smaller sympatric felids above a threshold that seems to be >0.1 ind./km^2. In the meantime, neither puma nor jaguar densities showed any effect on either ocelot or small cats' densities (De Oliveira et al. 2010, 2021).

Occupancy models have been applied in ocelots to understand how habitat use is modulated by a set of either site or landscape-scale predictors (Boron et al. 2020; García-R et al. 2019; Pasa et al. 2021), to estimate the true occupancy of a defined sampling area (Wang et al. 2019), or to find better ways to improve their detectability (Cove et al. 2014). Ocelot occupancy seems to positively respond to areas with dense vegetation, high prey availability, low poaching pressure, and with few or no presence of dogs or large felids (Fornitano et al. 2022; Massara et al. 2018; Moreno-Sosa et al. 2022; Wang et al. 2019). Detectability in ocelots has been found to increase when cameras are placed on roads rather than on trails, and to decrease with elevation (De Oliveira et al. 2022; Di Bitetti et al. 2010; García-R et al. 2019; Wang et al. 2019). Ocelots were more easily detected with visual attractants (hanging compact disks) compared to olfactive ones (cologne and sardines in oil), as they rely more on visual cues while active in their habitats (Cove et al. 2014). The detectability of ocelots was found to vary between 0.13 (Cruz et al. 2018) in degraded Atlantic Forests to 0.40 in island forest remnants created by hydroelectric dams in Central Amazonia (Benchimol and Peres 2015).

Hierarchical modeling research provides evidence-based arguments to facilitate and/or improve the conditions required by ocelots at both habitat and landscape scales, thereby recognizing its potential in conservation planning (Massara et al. 2015; Wang et al. 2019). International alliances to fill our knowledge gaps in regions with sparse or no information of ocelot density and occupancy will improve the form in which ocelots can be directly linked to the welfare of local communities and biodiversity maintenance. This is important because of the recognized role that ocelot populations play in the viability of conservation programs for other small Neotropical felids (De Oliveira et al. 2010, 2022; Cruz et al. 2018).

2.4.8 Leopardus colocolo

The Pampas cat is one of the least studied felids in the world, particularly for those populations inhabiting Andes, Cerrado, Pampa, and Mediterranean ecosystems. There are only very few studies available for this species complex, despite its wide distribution in Ecuador, Peru, Bolivia, Brazil, Chile, Argentina, Paraguay, and Uruguay. Spatially explicit models have been used to estimate population density in northwestern Argentina (Jolly–Seber model; Gardner et al. 2010) and in the central Bolivian altiplano (SECR, Huaranca et al. 2019). Also, the occupancy approach has been applied in the Brazilian savannas (Lima 2020), and in Sajama National Park, Bolivia (Huaranca et al. 2022). Density in the Argentina/Bolivia border area was considerably high for a small Neotropical felid, with estimates ranging from 0.74 to 0.78 ind./km^2 (Gardner et al. 2010), but in central Bolivia density estimates ranged between 0.053 and 0.089 ind./km^2 (Huaranca et al. 2019). It is unclear if this is due to the type of model used or ecological conditions. This last estimation is similar to that of the Andean cat in the same study area in Bolivia. Another study in the fringe of the Pampas region of Argentina reported 11.34–17.58 ind./km^2 in an area of 24.2 km^2, which can be considered small (Caruso et al. 2012). On the other hand, three studies of pampas cat occupancy have been reported, one where its occupancy increases with decreasing canopy cover, typically confirming the association of this species complex with open habitats (Lima 2020), and other where the increase in small mammal abundance was positively associated to the occupancy of pampas cats, whereas an increase in livestock abundance, mountain vizcacha abundance, distance to water, and grassland cover were negatively associated to it (Huaranca et al. 2022). In a third study in the Chilean Mediterranean ecoregion, *L. colocolo* did not show spatial avoidance with *L. guigna* and its occupancy was associated with shrubland and forested ravines when free roaming dogs were not detected (Beltrami et al. 2023). Also, the habitat associations found using HM and described here may be species-specific and cannot be generalized to all the species in the *L. colocolo* complex (see evidence for this in Nascimento et al. 2021 and Tirelli et al. 2021). The most likely acceptance of current subspecies as five separate taxonomic units (Nascimento et al. 2021) will make research on all species a priority as coverage will be further reduced.

2.4.9 Leopardus wiedii

The margay is often regarded as a felid with arboreal habits; thus, it is often associated with forest cover, including large continuous evergreen forests and small forest fragments in open landscapes (De Oliveira et al. 2015; Meira et al. 2018). Almost all margay studies included in our review were conducted either in the Atlantic Forest or in the Amazon. Margay density estimates through SCR models were conducted in the southernmost Atlantic Forest, ranging from 9.6 to 37.4 ind./100 km^2 (Horn et al. 2020), and in the Ecuadorian Amazon ranging between 0.0 and 19.1 ind./100 km^2 (Gil-Sánchez et al. 2021). In both areas, margay density was higher in better protected areas with higher forest cover. In the Ecuadorian Amazon specifically, margays were the small felids with the highest density reduction in response to increased anthropogenic pressure (Gil-Sánchez et al. 2021). Furthermore, occupancy studies in the northwestern Amazon and in the Brazilian Atlantic Forest documented higher margay occupancy in areas with higher protection levels (Mena et al. 2020; Nagy-Reis et al. 2017). Throughout several Neotropical sites (including two outside South America), margay occupancy consistently increased with a higher Normalized Difference Vegetation Index (Contreras-Díaz et al. 2022). A major overarching conclusion from these HM studies is that margays are highly dependent upon forest and tree cover. Based on our review, we also highlight the existence of research gaps for margays at several ecoregions. Areas such as the Andean cloud forests or the Uruguayan savannas are known to harbor margay populations (Migliorini et al. 2018; Vanderhoff et al. 2011), the latter being the southernmost limit of the species distribution (De Oliveira et al. 2015). HM studies addressing margay abundance or occupancy at some of these areas are lacking and would be helpful for establishing baselines for conservation interventions. With regard to the potential threat from domestic species, one study explored the relationship between introduced wild pigs and margays in the Atlantic Forest through multispecies occupancy models (Hegel et al. 2019). There, wild pigs exerted a negative effect on margay occupancy, presumably from vegetation degradation. Similar studies should be conducted, testing the effect of domestic dogs on margay habitat use patterns.

2.5 Conclusions

This review may be helpful to show that we need to use reliable and standardized methods, robust survey and data collection design, reliable analytical methods, and relevant hypotheses that test ecological/conservation aspects such as habitat, sympatric species, human impact, threats, and adaptation strategies. Finally, priority should be given to species and geographical areas for which there is no information.

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Chapter 3
Patterns of Occupancy and Density of the Small Felids of Tropical America

Lester Alexander Fox-Rosales, Juan Camilo Cepeda-Duque, and Tadeu G. de Oliveira

Abstract The Neotropical realm harbors 9–14 species of small- and medium-sized felids, depending on taxonomic schemes. Some of these species are poorly known, and a few of them are globally threatened. Hierarchical models (HMs) have been developed to consider imperfect detectability in the process of modeling abundance and occupancy, thereby allowing for less biased inferences. Because of this, HMs have been applied to some of the Neotropical felids. Here, we conducted a literature review on abundance and occupancy studies conducted on small-/medium-sized felids of Tropical America. We found that most studies of abundance and occupancy have focused on ocelots (*Leopardus pardalis*), while the other species were mostly in multispecies studies. Tree cover was found to be influential for the occupancy of ocelots and tiger-cats (*L. tigrinus*), with jaguarundis (*Herpailurus yagouaroundi*) selecting areas closer to water and being less associated with dense vegetation cover. Density estimates through spatially explicit capture models were conducted on ocelots, margays (*L. wiedii*), and tiger-cats, with ocelots exhibiting densities much higher than the two smaller felids. We conclude by suggesting sampling schemes specifically targeted toward small felids abundance or occupancy, as several studies include these species as by-catch.

Keywords Hierarchical model · Jaguarundi · Margay · Northern tiger-cat · Ocelot

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3.1 Introduction

The Neotropical region is rich in species of small- to medium-sized felids. Depending on taxonomic schemes and not including the bobcat, there are between 9 and 14 species found in tropical America (Kitchener et al. 2017; Nascimento et al. 2021). For the sake of simplicity, here we follow the taxonomy proposed by Kitchener et al. (2017). Therefore, we focus mostly on the medium-sized ocelot (*Leopardus pardalis*, 10 kg), the small-sized jaguarundi (*Herpailurus yagouaroundi*, 4 kg), the pampas cat (*Leopardus colocola*: including *L. garleppi, L. braccatus*, 3 kg), the margay (*Leopardus wiedii*, 2.5 kg), the southern tiger-cat (*Leopardus guttulus*, 2 kg), and the northern tiger-cat (*Leopardus tigrinus*: including *L. tigrinus* – savanna tiger-cat, *L. pardinoides*, and the clouded tiger-cat; 2 kg) (Fig. 3.1).

These species are sympatric across most of the Neotropics, with the ocelot, margay, and jaguarundi being found in all countries from Mexico as far down as Argentina. The tiger-cats range as far north as Costa Rica, while the pampas cat is found in the open biomes of tropical America. Some of the species are threatened at

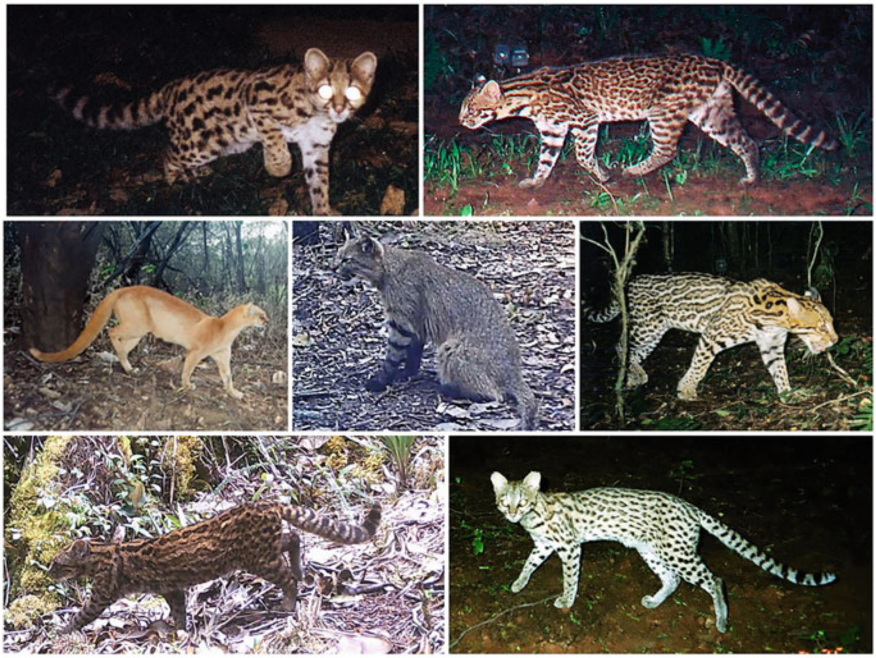

Fig. 3.1 Camera-trap images of the focal species/taxonomic units, from top to bottom, from left to right: margay (*Leopardus wiedii*), southern tiger-cat (*Leopardus guttulus*), jaguarundi (*Herpailurus yagouaroundi*), pampas cat (*Leopardus colocola/braccatus*), ocelot (*Leopardus pardalis*), clouded tiger-cat (*Leopardus [t.] pardinoides*), and savanna tiger-cat (*Leopardus [t.] tigrinus*). (©Wild Cats Americas Conservation Program)

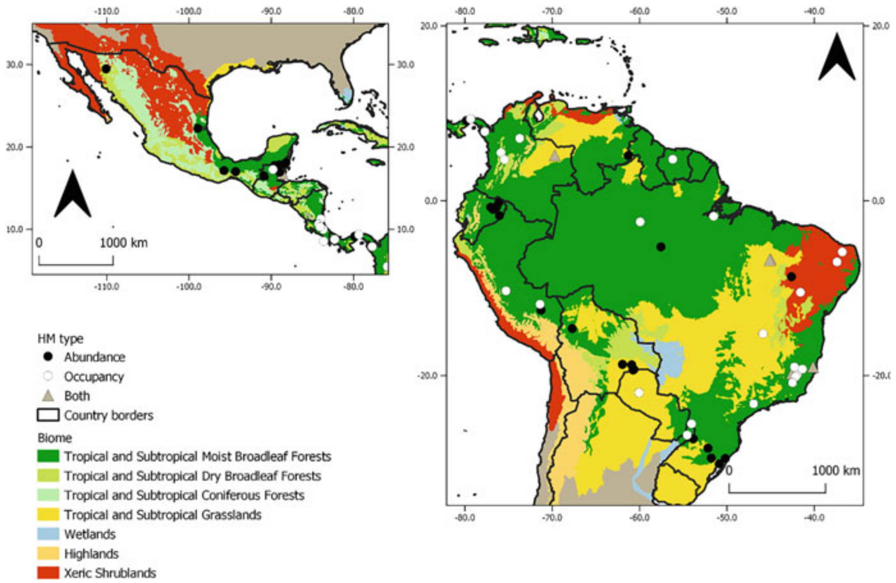

Fig. 3.2 Location of study sites in which HMs were used to analyze abundance and/or occupancy of small Neotropical felids

either the national or global level, with both tiger-cat species being classified as Vulnerable (de Oliveira et al. 2016; Payan and de Oliveira 2016), and margays and pampas cats as globally Near Threatened (de Oliveira et al. 2015; Lucherini et al. 2015). Moreover, some of these species are poorly known, with no published density estimates for southern tiger-cat and only one for northern tiger-cat, for example. All these factors make the small Neotropical felids a group in need of ecological studies. Abundance and occupancy estimates, in particular, can provide much-needed data for conservation assessments.

The use of hierarchical models (HMs) to make inferences on ecological processes, such as species abundance and occurrence, has become ubiquitous in recent years. These models are characterized by one or more submodels or levels; one describing the observation process (detectability) and the other describing the ecological process (species abundance or occurrence). HMs have been extensively applied to the small Neotropical felids, mostly to obtain density estimates and occupancy data. By incorporating data on the detectability process, HMs allow less biased inferences on abundance and occupancy than detection-naïve approaches (Kéry and Royle 2015).

In this chapter, we intend to provide an overview of what is known about occupancy and density estimation of the small to medium-sized felids found in the tropical parts of the Neotropics (Fig. 3.2). A summary of published works for each hierarchical model type is provided, as well as survey recommendations that are specific to small Neotropical felids.

3.2 Methods

We conducted a literature review of camera-trapping studies addressing small Neotropical felid abundance and occurrence through hierarchical models. We define our study region as the tropical and subtropical regions of Latin America, specifically from México to Argentina, and excluding Chile and Uruguay. For the pampas cat (*L. colocola*), we limit our inference to the proposed *L. braccatus* species (Nascimento et al. 2021) in the Brazilian savannas. For the northern tiger-cat group, we considered both the savanna tiger-cat (*Leopardus [t.] tigrinus*) and the clouded tiger-cat (*Leopardus [t.] pardinoides*).

3.2.1 Study Area

We defined our study area as the tropical and subtropical ecoregions from Mexico to northern Argentina (Fig. 3.2). Our ecoregions are based on the *Terrestrial Ecoregions of the World*, defined by the World Wildlife Fund (Olson et al. 2001). We grouped all ecoregions in Mexico and Central America as the Mesoamerican region due to the low number of studies per ecoregion there. This includes lowland forests, clouded forests, and matorral ecoregions in northern Mexico. In South America, we grouped all the Amazon ecoregions into the Amazon region. We also grouped the Caatinga scrub and Cerrado savannas into the Brazilian drylands. Furthermore, we grouped all Andean Forest ecoregions into the Andes region. It is worth noting that we excluded the Puna and Andean deserts. Finally, we treated the Atlantic Forest biome as a single region.

3.2.2 Literature Review

We conducted a literature review using the Web of Science and Google Scholar to identify hierarchical model studies done on small Neotropical felids. We only included camera-trap studies. We included peer reviewed publications, book chapters, as well as theses and gray literature. Some of the data used were not available on searchable databases and instead came from unpublished work done in the senior author's research group. Our searches included keywords in English, Spanish, and Portuguese including species names and hierarchical model types. Besides studies focused on either of the seven felid species, we included multispecies studies in which at least one of the felid species was involved.

For each study, we recorded the geographic coordinates, and whether the study dealt with abundance, occupancy, or both. We obtained parameter estimates (abundance, density, occupancy, detectability, colonization, extinction) and associated uncertainty measures (standard error and confidence intervals whenever given). We grouped single-season occupancy studies by region. Other HM studies were analyzed by HM type due to the low number of studies per HM model. Finally, we identified research gaps and future recommendations.

3.3 Single-Season Occupancy Models

3.3.1 Mesoamerica

Occupancy studies specifically targeting small felids in the Central American isthmus were not found. Nevertheless, there are a few community-occupancy studies in the region that include small felid species in their samples. These studies often address the issue of deforestation or remaining forest cover in biological corridors (Salom-Pérez and Corrales-Gutiérrez 2021) or across entire countries (Meyer et al. 2020). One gap that was identified is that most of these studies only include the ocelot due to extremely low detections of margays and jaguarundis. Furthermore, six out of eight studies addressing small felids occupancy through single-season models in the isthmus were conducted either in Costa Rica or Panama. A major research gap in HMs targeting smaller felids exists in northern Central America, which is where the largest areas of lowland rainforest remain.

Ocelots in Mesoamerican study sites show a strong preference for dense forest cover. In southeastern Nicaragua, for example, ocelot occupancy was found to be higher within or near protected areas and in areas with low levels of deforestation (Jordan et al. 2016). In the Barbilla-Destierro corridor in eastern Costa Rica, ocelots were the only small-cat species to be significantly affected by forest cover, with occupancy strongly increasing with higher cover (Salom-Pérez and Corrales-Gutiérrez 2021). Sympatric jaguarundis and margays in the same study site did not exhibit a significant response to this covariate. In the Mamoní Valley, Panamá, ocelot occupancy was most influenced by primary and secondary forest cover (Moreno-Sosa et al. 2022). Conversely, along an altitudinal gradient of 3000 m in the Volcán Barva TEAM site (northeastern Costa Rica), ocelot occupancy was not affected by canopy height (higher values are typical of dense lowland rainforest). Instead, elevation was the only spatial covariate that had a significant effect on ocelot occupancy, with the species preferring lowlands over highlands (Ahumada et al. 2013). One major takeaway in several studies is that ocelots consistently rank in the upper zone of occupancy values, even when compared to other noncarnivorous taxa. In the logging concessions of northeastern Guatemala, at 96%, ocelots exhibited the highest occupancy probability of any medium to large-sized mammal (Tobler et al. 2018). At that same site, margays and jaguarundis had lower occupancy probabilities than both jaguars and pumas. Similarly in the Montes Azules Biosphere Reserve of southeastern México, ocelots had the highest occupancy of all felids (Gil-Fernández et al. 2017).

In the Osa Peninsula of Costa Rica, Vargas-Soto et al. (2022) implemented a community-occupancy model on medium- and large-sized vertebrates, including ocelots, jaguarundis, and margays. They used variables such as the proportion of primary forest cover and the human modification index proposed by Kennedy et al. (2019) to compare vertebrate communities in protected and nonprotected areas of the peninsula. An interesting finding was that jaguarundi occupancy increased by 364% in more disturbed areas, a bigger increase than that of raccoons (132%) and only surpassed by that of four-eyed opossums (665%). It is worth noting however that the entire survey area only had low to moderate levels of anthropogenic disturbance. Another point is that the jaguarundi is mainly an open-habitat species, and is less common in forested areas (de Oliveira 1998). Among the three small felid species present at the site, only margays exhibited a significant positive response to the proportion of primary forest cover.

Finally, few studies have addressed the effect of roads on felid occupancy in the region. Across Panama, the distance to paved roads was the only variable found to affect ocelot occupancy, with the species significantly preferring areas away from roads (Meyer et al. 2020). Other variables, such as the distance to the nearest village or the percentage of forest cover, did not influence the species. However, margays and jaguarundis were not included in that study. Finally, in Guatemala, ocelot detectability was significantly higher on active logging roads than on old roads or areas away from roads (Tobler et al. 2018). Margays and jaguarundis did not respond to any of the three road types. The key difference between both studies is that Meyer's was conducted countrywide while Tobler's was based on a logging concession where poaching is prohibited. Logging roads act as man-made trails and facilitate movement inside dense forests, thus increasing the probability of detection.

3.3.2 The Andes

The available occupancy studies for small felid species in the northwestern Andes have been mainly focused on the highland cloud forests of the western Andes as well as the lowland rainforests of the Magdalena and Cauca basins. At one end of the elevation continuum, there are few studies about how the occupancy and detection of clouded tiger-cats, ocelots, margays, and jaguarundis in the highland cloud forests have been affected by different factors such as human disturbance, landscape, and microhabitat structure. Clouded tiger-cats have shown moderate to high occupancy in the highland cloud forest but are relatively difficult to detect. A study conducted in the Mesenia-Paraminllo Nature Reserve showed that clouded tiger-cat detectability increased with greater moisture in the forest floor, which is often related to greater productivity (Bonilla-Sánchez et al. 2020). Andean cloud forests at middle elevations (2500 m) are mainly used by clouded tiger-cats in several protected areas of the Middle Cauca. This is crucial for understanding how their populations will respond to both climate and land-use changes in the region (Cepeda-Duque et al. 2023). This species has proven to be resilient to different degrees of habitat fragmentation both within (Cepeda-Duque et al. 2023) and outside (Bedoya-Durán et al. 2021) protected areas. This does not necessarily apply to ocelots, as another study claims that this species negatively responds to edge effects in highland cloud forests in Colombia (García-R et al. 2019). Moreover, ocelot detectability seems to be negatively affected by elevation and appears to be rare in the region at elevations above 1900 m (García-R et al. 2019).

At the other end of the elevation continuum, research has been focused on the lowlands of the Magdalena River basin to understand the impacts of oil palm plantations on the occupancy of ocelots and jaguarundis (Boron et al. 2018, 2019; Pardo et al. 2019). In terms of detectability, placing cameras on trails significantly improved ocelot detection (Boron et al. 2019). In one study, ocelots were the only felid that used oil palm plantations, likely as a response to increased rodent availability and because of the absence of large predators such as jaguars and pumas (Boron et al. 2018). Conversely, another study showed that ocelots were more often associated with natural forested areas (Boron et al. 2019). The detectability of jaguarundis was found to increase in oil palm plantations, although the authors recognize that such findings need to be cautiously interpreted, as the standard errors of their estimations were large. It appears that, insofar as a given habitat presents a minimum forest structure (e.g., oil palm plantations) and enough availability of prey, both ocelots and jaguarundis can thrive in this lowland human-degraded landscape of the Magdalena River basin. Another point that could affect the detectability and occupancy patterns of the jaguarundi and other small cats could be the negative impact of ocelot numbers above a threshold upon which it affects the abundance and land-use patterns of the smaller species, which is known as the "ocelot effect" (Dias et al. 2019a; de Oliveira et al. 2021a, b; Gonçalves 2022).

3.3.3 Brazilian Drylands (Caatinga and Cerrado)

Of the smaller felid species, northern tiger-cats are the ones that have the greatest number of occupancy studies in the Caatinga domain. An interesting pattern emerges from these studies, which is the species' preference for forested environments and denser vegetation in this semiarid landscape. In a survey of 10 study sites in the Caatinga of Rio Grande do Norte, Marinho et al. (2018) discovered that forest cover had a significant positive effect on the species' occupancy. The same result was found by Fox-Rosales and de Oliveira et al. (2022) at the Tamanduá Ranch in the state of Paraiba, where tiger-cats used the forested areas more than the remaining Caatinga formations available at the site (shrublands and thorny scrub). Sympatric jaguarundis at the same site did not exhibit a preference for either vegetation type, thus highlighting the species' flexibility and its ability to use habitats with varying degrees of vegetation cover.

Due to a semiarid climate, water is likely to be a limiting factor in species distribution and habitat use patterns in the Caatinga. However, of the studies that tested the effects of this variable on species occupancy and detectability, only Dias et al. (2019a, b) found significant results for some of the felid species. Their study, conducted in the Boqueirão da Onça region, analyzed the occupancy patterns of several carnivore species concerning water availability and human activity (distance to settlements, wind farms, cattle, domestic dogs, and poachers). They found out that the jaguarundi was strongly affected by distance to water sources, with significantly higher occupancy and detection in areas closer to water. Sympatric ocelots had higher detectability near water sources as well; however, this variable did not influence species occupancy. The variable did not influence the occupancy or detectability of northern tiger-cats in the area. In the Caatinga of Rio Grande do Norte, distance to water sources did not influence northern tiger-cats' occupancy or detectability either (Marinho et al. 2018). Despite this apparent lack of influence of water sources on felid occupancy patterns, it is worth noting that all these studies used permanent water sources as their variable. In the Caatinga, water from rain often accumulates in intermittent rocky pools (locally known as *lajedos*), which represent an important water source for wildlife. Future studies should include these intermittent water sources as variables in the models.

With increasing habitat loss in the Caatinga, it is important to measure the potential effects of human activities on the species' occupancy patterns. Most studies of small felid occupancy in the biome have incorporated variables such as distance to settlements, habitat edges, paved roads, and even wind farms (Dias et al. 2019a). The effects of these variables on small felids appear to be context specific. For instance, in Rio Grande do Norte, northern tiger-cats strongly avoided areas closer to agrarian settlements (Marinho et al. 2018). At the Tamanduá Ranch, this same variable did not influence tiger-cat occupancy and, in fact, it had a significant negative effect on jaguarundi occupancy, that is, species preferred sites closer to households (Fox-Rosales and de Oliveira 2022). This discrepancy comes from the fact that, at the Tamanduá Ranch, poaching is prohibited, and domestic dogs are required to be permanently leashed. In this case, settlements per se do not represent a threat to wild felids. Furthermore, these households lie in areas adjacent to plantations and old fields, which may provide the felids with a prey base (Rajaratnam et al. 2007). Thus, this could explain why jaguarundis have higher occupancy near settlements at that particular site.

Nevertheless, throughout the entire biome, human activities do negatively impact small felids. In Boqueirão da Onça, ocelots exhibited a higher detection probability in areas farther away from settlements (Dias et al. 2019a, b). Jaguarundi occupancy was also higher in areas away from settlements at this site. Incidentally, the species' detectability was higher closer to wind farms, an increasing form of disturbance in the Caatinga. This study at Boqueirão da Onça also attempted to measure the effects of poaching and domestic dogs on the occupancy and detectability of the felid species. Neither variable was found to significantly influence the parameters of either jaguarundis, savanna tiger-cats, or ocelots. At another site in the Caatinga, at Tamanduá Ranch, although spatial overlap between domestic dogs and savanna tiger-cats was high, the first did not influence either occupancy or detectability of the latter (Fox-Rosales and de Oliveira 2023). However, this does not mean that these variables do not pose a threat to small felids in the region. The main threat from domestic dogs would be pathogen transmission, which could happen if domestic dogs and native felids share the same space. So far, there are no published studies on the Caatinga that address the interaction between domestic dogs and small felids.

There have only been two studies conducted so far that considered small cat occupancy in the savannas (Oliveira 2018; Lima 2020). As for the semiarid Caatinga, occupancy of the tiger-cat in the northern Brazilian savannas was positively influenced by vegetation cover and negatively influenced by proximity to human households. The pampas cat, on the other hand, showed higher occupancy in open savannas. The difference in habitat use of the pampas cat and tiger-cat generates a spatial segregation of the species (Lima 2020). In the protected area around Grande Sertão Veredas National Park, in Minas Gerais, ocelots were positively influenced by the area's protected status and negatively influenced by the savanna formations. Conversely, for tiger-cats, no covariate affected either occupancy or detectability. This even included testing the effect of the dominant mesopredator (ocelot) over the tiger-cat. The low density of ocelots in the study area was likely related to the lack of its effect on savanna tiger-cat occupancy and detectability (Oliveira 2018).

3.3.4 Atlantic Forest

There have been several studies on the occupancy patterns of small felids in the Atlantic Forest, with particular interest in the ocelots. A common theme in these studies is that of addressing species occupancy patterns within the highly fragmented context of the Atlantic Forest. Hence, they include covariates such as distance to a protected area or proportion of croplands and plantations. In Iguaçu National Park, Da Silva et al. (2018) tested the effects of distance to edges, proximity to tourism infrastructure, and hunting pressure on the occupancy and detectability of several mammal species. They found that ocelot occupancy was higher in areas away from the park's edge, with jaguarundis exhibiting the opposite pattern. Both species exhibited higher detection rates near tourism infrastructure, which the authors attribute to the fact that felids may use the same trails that tourists use. Neither of the two species responded to hunting pressure. At Serra do Japi, both ocelots and margays had higher occupancy probabilities near the main protected area (Nagy-Reis et al. 2017). This illustrates the importance of protected areas for small and medium-sized felids in the Atlantic Forest.

A key issue for the long-term conservation of small felids in the Atlantic Forest is maintaining connectivity between forest fragments. Roughly 80% of the remaining forest patches in this biome are of less than 50 ha (Ribeiro et al. 2009). In one study spanning several protected areas, ocelot detectability was found to be higher in areas with eucalyptus plantations (Massara et al. 2018). This suggests that the species can use such plantations to move between patches of native forest. Unfortunately, there have been no studies testing the effect of fragmentation on other small felids abundance or occupancy in the Atlantic Forest. This could be an important research priority.

3.4 Multiseason Occupancy Models

In light of the population closure assumption of the standard occupancy model, a multiseason model that estimates site colonization (γ) and extinction (ε) probabilities has been proposed (MacKenzie et al. 2003). We found three instances of this dynamic occupancy model being applied to small Neotropical felids (ocelots, margays, and jaguarundis) in Costa Rica (Ahumada et al. 2013); ocelots and jaguarundis in the Atlantic Forest (Da Silva et al. 2018); and margays in Belize (Harmsen et al. 2017). However, only the first three studies had the goal of estimating turnover rates across the sampling period to explore occupancy trends.

The study in Costa Rica was conducted at the Volcán Barva Tropical Ecology Assessment and Monitoring site, a 30-km strip of forest spanning a 3000-m elevational gradient, ranging from lowland tropical rainforest to cloud forest and highland vegetation. Using a 5-year dataset, the authors applied dynamic occupancy models to 13 species of medium to large-sized mammals that included ocelots, margays, and jaguarundis. The authors implemented models with site covariates for occupancy (canopy height, elevation, forest type, and distance to edges) and year-specific colonization, extinction, and detection. Only ocelots showed a significant response to site covariates, with occupancy declining as elevation increased (Ahumada et al. 2013). Margays and jaguarundis showed year-specific colonization, extinction, and detection probabilities. Overall, all three species maintained a stable occupancy trend during the 5 years. Nevertheless, the authors note that occupancy estimates for margays and jaguarundis were not precise, due to low detections, so their results should be interpreted with caution.

In Iguaçú National Park, Brazil, both single- and multiseason occupancy models were run for several mammalian species, including ocelots and jaguarundis. The sampling was conducted between 2009 and 2014 (with a gap from 2011 to 2013) using 37 camera sites spaced approximately 4 km apart (Da Silva et al. 2018). Overall, ocelots showed stability in occupancy across the survey period, while jaguarundi occupancy increased with respect to the first year. Detectability of both species was higher in areas farther away from the park's edge. Jaguarundis had the lowest detection probability of all species assessed ($p = 0.05 \pm 0.02$). No covariates were used to model γ and ε in this study, and no estimates for those parameters are given. The authors do not go into further detail about the patterns found for the small felids.

Finally, in Belize, the dynamic occupancy model was applied to margays to investigate detection patterns in the Cockscomb basin from a 12-year dataset (Harmsen et al. 2021). In this study, the authors interpreted model results in the context of camera placement suitability for margays, such that high fluctuations of γ or ε across primary periods suggest suboptimal camera placement for the species. Margays exhibited a fairly constant detection probability across the 12-year dataset, but wide occupancy fluctuations that ranged from 0.16 to 0.89 for the whole study period. The authors concluded that the camera-trapping grid, designed for jaguar monitoring, was not adequate for monitoring margays. They recommend a shorter intertrap spacing interval (<1 km), and sampling of narrower trails (<1.5 m wide).

It has been suggested that accurate estimation of turnover rates from dynamic occupancy models requires at least 120 sampled sites (Mckann et al. 2013). Unfortunately, such samples are uncommon in camera-trapping studies in the Neotropics, let alone for periods long enough to allow for population processes to occur. Researchers working with data on small felids collected over several years may use other alternatives. If the goal is to evaluate species–habitat associations in an occupancy-modeling framework, one option could be to stack the data in such a way that each site–year combination is different from one another (MacKenzie et al. 2017). This approach has been applied to all the small Neotropical felids (Fox-Rosales and de Oliveira 2023; Jordan et al. 2016; Santos et al. 2019). If estimating turnover rates is the final goal, then we recommend optimizing surveys for the target species, maximizing detectability, and prioritizing repeated sampling of sites across seasons/years, instead of increasing the spatial extent of sampling (Fuller et al. 2016).

3.5 Co-occurrence Models

Several multispecies occupancy models have been developed to address questions of species co-occurrence (Mackenzie et al. 2004; Richmond et al. 2010; Rota et al. 2016; Waddle et al. 2010). Given the high niche overlap between small Neotropical felids, the potential for interspecific competition is very high, and multispecies occupancy models provide a venue for addressing questions of spatial segregation among species. In most cases, the multispecies model used was the one proposed by Mackenzie et al. in 2004. However, another approach that has been used is to estimate the conditional occupancy of the dominant species and use it as a variable on the occupancy of the subordinate one. Conditional occupancy is defined as the occupancy of the dominant species given the observed data (Richmond et al. 2010). Using this approach at several small sites in the Atlantic Forest, ocelots were not found to constrain space use of southern tiger-cats or that of other sympatric mesopredator species (Massara et al. 2016). Nevertheless, as observed by de Oliveira et al. (2021a, b), for ocelots to constrain the smaller species, their abundance has to be above certain thresholds, without any effect expected at low abundance.

At Serra do Japi, in the Brazilian Atlantic Forest, co-occurrence of ocelots, margays, and southern tiger-cats was addressed via single-season, two-species occupancy models (Nagy-Reis et al. 2017). Ocelots were considered dominant over both smaller species, and margays were considered dominant over southern tiger-cats. Via this model, the authors calculated the species interaction factor (SIF) for each species pair with $\text{SIF} = 1$ being indicative of both species occurring independently, $\text{SIF} > 1$ suggests aggregation, and $\text{SIF} < 1$ suggesting avoidance. The results found suggested no negative effect of either species on each other, with $\text{SIF} = 1$ for occupancy of each species pair and $\text{SIF} = 1.11–3.53$ for detectability of each species pairs. In Atlantic Forest sites in northeastern Argentina, a negative relationship between ocelots and southern tiger-cats was found, with a SIF = 0.47 (Cruz et al. 2018). There, southern tiger-cat occupancy declined in the presence of ocelots. Interestingly, this pattern exhibited variation according to vegetation types, with southern tiger-cats avoiding ocelots to a greater degree in pine plantations than in continuous forests. Overall southern tiger-cat occupancy was highest at sites with low to no ocelot occupancy. These sites were covered by forest with an intermediate degree of disturbance, whereas, at the most pristine sites, ocelots were the most abundant felid. Margays and jaguarundis were excluded from the occupancy analyses in this study due to a low number of records. Nevertheless, records of both species were higher in forest fragments than in continuous forest. These results, however, do not take into account the actual numbers of individuals of each species using the areas. At low abundance, species are not expected to influence one another (Levi and Wilmers 2012). In tropical America, only ocelots are expected to exert dominance over the other mesocarnivores, and no influence of the other small cat species should occur on each other (de Oliveira et al. 2021a).

Finally, across several sites in the Amazon basin, margay occupancy was found to decline with increasing ocelot occupancy, with the SIF = 0.62 (Gonçalves 2022). Margays responded differently to elevation depending on whether or not ocelots co-occurred in the area. In areas where ocelots were present, margays preferred lower elevations; while, in areas where ocelots were absent, margay occupancy increased with elevation (Gonçalves 2022). Overall margay occupancy was lower in areas where ocelots were present.

An important takeaway from these studies is that the scale of the study matters extensively in the results. Both studies that showed antagonism between ocelots and smaller felids (Cruz et al. 2018; Gonçalves 2022) were conducted at several sites over a large environmental gradient. On the other hand, the studies that suggested "aggregation" among small felids (Boron et al. 2018; Massara et al. 2016; Nagy-Reis et al. 2017) were conducted at smaller study sites with fewer forest fragments. Spatial avoidance is more difficult to show at these sites via occupancy models. With lower habitat availability, different species are likely to use the same sites, though at different times or periods. Two species may overlap spatially when in fact one may be avoiding the other at the temporal scale. Subordinate species may also leverage the dietary niche dimension to avoid competition. At several small Atlantic Forest sites for example, the southern tiger-cat's habitat use was not affected by ocelot occupancy, instead, the species exhibited high levels of diurnal activity and, hence, low temporal overlap with ocelots (Massara et al. 2016).

Regarding spatial interactions among the smaller felids, the multispecies occupancy model proposed by Rota et al. (2016) has been applied to northern tiger-cats and jaguarundis at the Tamanduá Ranch in the semiarid Caatinga (Fox-Rosales and de Oliveira 2023). Unlike other multispecies occupancy models, Rota's parameterization does not require defining a priori dominance status among species pairs (Rota et al. 2016), which makes it suitable for addressing co-occurrence of species pairs in which there is no clear dominance hierarchy. In the Caatinga, northern tiger-cats and jaguarundis often occur in areas where ocelots are absent. At the Tamanduá Ranch, both species exhibited positive co-occurrence, which increased in the presence of the others regardless of the amount of tree cover or distance to plantations. Instead, both species segregated temporally, with jaguarundis being diurnal and tiger-cats nocturnal (Fox-Rosales and de Oliveira 2023).

So far, no multispecies occupancy model has taken into account the differences in abundance between each species. This is because occupancy only considers detection/no detection data, not counts of individuals. Coabundance is another interesting field that has hardly been explored, especially because of how complicated it is to estimate species abundance with camera traps. Additionally, co-occurrence patterns are not always a reflection of interactions, which is a long-standing and widely discussed issue (e.g., Gompper et al. 2016; Blanchet et al. 2020; Farris et al. 2020; Andrade-Ponce et al. 2022). Furthermore, models also do not consider the fine-scale temporary partitioning that may arise from the presence of a competitor (i.e., subordinate species may use the same site as the dominant one, but either at a different time of the day or in a different period altogether). Recently developed multispecies occupancy models with a continuous time-detection process represent a fruitful future direction for addressing spatial and temporal co-occurrence of small Neotropical felids (Kellner et al. 2022; Parsons et al. 2022).

3.6 Density

3.6.1 Spatially Explicit Capture–Recapture Models

Spatially capture–recapture (SCR) models have become ubiquitous during the last decade. They use data from animals with markings, such as spotted and stripped patterns, to estimate density through spatially explicit recaptures. However, they have not been extensively applied to the Neotropical small cats, and most studies have focused on ocelots. Two studies in the Atlantic Forest and Ecuadorean Amazon addressed margay densities via SCR models. The latter also addressed jaguarundis. Finally, one study in the Cerrado obtained density estimates for the northern tiger-cat via SCR models.

Ocelot density studies, using spatial capture–recapture models, span a wide range of the species distribution, including sites in northeastern México, Belize, central Panamá, the Amazon, Magdalena Valley, Orinoco Plains, the Caatinga, and the Atlantic Forest. Ocelot densities were found to be highly variable across the whole range. Previous works suggest that ocelot density is correlated with tree cover and temperature (de Oliveira et al. in press) as well as rainfall (Di Bitetti et al. 2008). Ocelot densities were lower in the highly degraded landscapes of the Magdalena River basin when compared to a flooded landscape of the Orinoco plains that had had little intervention (Boron et al. 2021). However, another study, also conducted in the Orinoco plains, found ocelot densities of 1.8 ind./100 km^2, which fall among the lowest reported densities in the ocelot SCR-density literature (Garrote et al. 2019). In terms of SCR densities, the highest values came from Barro Colorado Island (BCI),

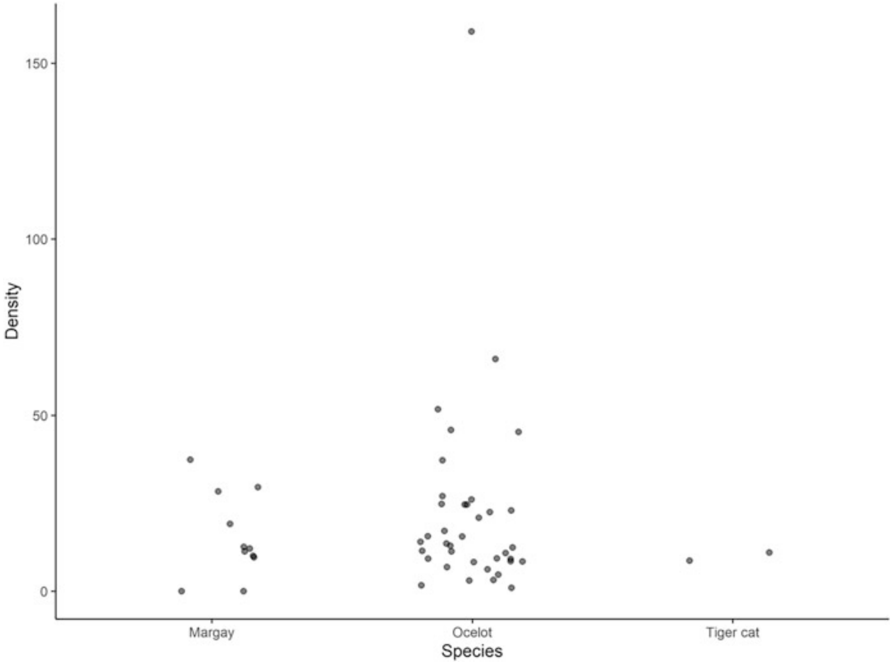

Fig. 3.3 Spatially explicit capture–recapture density estimates for ocelots, margays, and savanna tiger-cats

with an estimated density of 159 ± 46 ind./100 km^2 (Rodgers et al. 2014). This site is an outlier, as it is a 15-km^2 island in the Panamá canal, with ocelots being the largest mammalian predator present year-round. Barring BCI, the highest SCR densities of ocelots come from the Bolivian Amazon at 66 ind./100 km^2 (Ayala et al. 2010).

Margay densities estimated via SCR models came from two published studies. One conducted at several sites of the southernmost Atlantic Forest (Horn et al. 2020) and another one at sites with varying degrees of anthropic threats in the Ecuadorean Amazon (Gil-Sánchez et al. 2021). Margay densities in the Atlantic Forest ranged from 9.6 ± 6.4 ind./100 km^2 in areas with high human disturbance to 37.4 ± 15.1 ind./100 km^2 at the least disturbed site with high forest cover. Furthermore, the highest density came from a site at which ocelots are very rare (Horn et al. 2020). In this study, vegetation cover, measured by the normalized difference vegetation index, strongly influenced margay densities, with higher densities in areas with higher vegetation cover. The sex covariate also influenced the movement parameter of margays and was greater for males (1.19 km) than females (0.59 km), which is similar to what has been found for ocelots in the SCR studies that included a sex covariate for the movement parameter. The 37 ind./100 km^2 reported is considerably higher than the known values for small Neotropical cats (Horn et al. 2020; Figs. 3.3 and 3.4), even considering traditional CR models that always present much higher values than those of SCR.

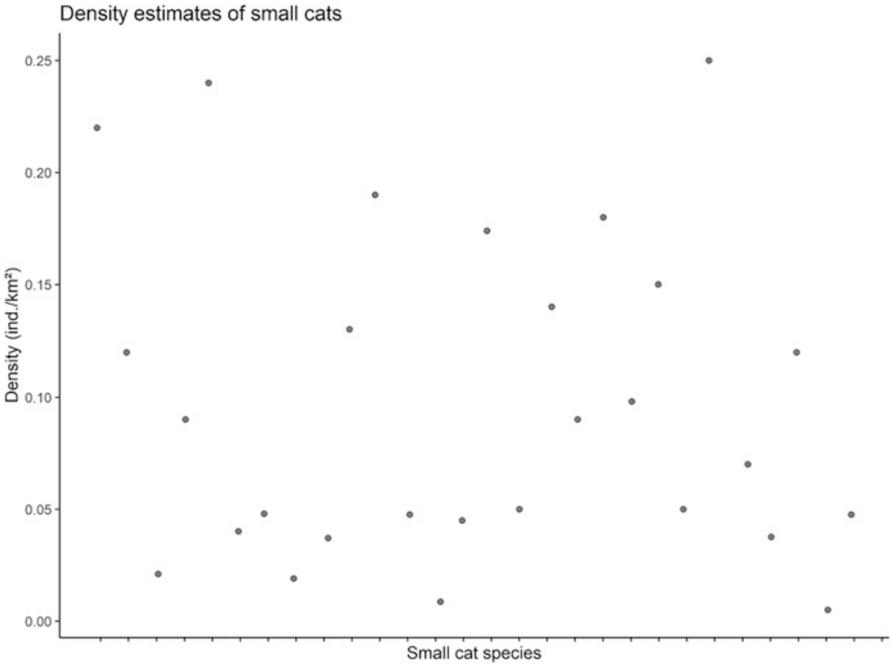

Fig. 3.4 Classic capture–recapture densities estimate of small cats from tropical America: jaguarundis, margays, northern tiger-cats, and southern tiger-cats. These are all densities in which ocelots are absent or rare. In most areas where ocelots are abundant, densities of small cats should be smaller than the lowest values presented here. (de Oliveira et al. 2020)

In the Ecuadorian Amazon, a total of seven sites (protected and unprotected) were surveyed and targeted the complete Amazonian felid assemblage (Gil-Sánchez et al. 2021). A range of 0–6 individual margays were identified per site, compared to 7–35 individual ocelots. Margay densities ranged from 0.00 to 19.10 ± 9.29 ind./100 km^2 and, at all seven sites, margay densities were lower than those for ocelots. In a similar result to the Atlantic Forest sites, margay densities in the Ecuadorean Amazon were constrained by forest loss. At two sites with high deforestation rates and human activities, margays were not detected. Jaguarundis also had their densities estimated in the Ecuadorian Amazon, with densities reported at 0.00–13.06 ± 7.88 ind./100 km^2, also using a Bayesian approach (Gil-Sánchez et al. 2021). The jaguarundi estimates were considerably high given the species' inherent rarity level in Amazonian forests (de Oliveira et al. in press) even when compared to those obtained by nonspatial analysis in other areas (de Oliveira et al. 2021b). Perhaps, this was a consequence of the low number of detections reported by the authors.

Finally, the other small felid species for which SCR estimates are available is the savanna tiger-cat. At Mirador State Park, in Brazil, densities were 8.7 ± 3.9 ind./100 km^2 (95% CI: 3.8–20 ind./100 km^2) at the Mel outpost and 11.0 ± 4.9 ind./100 km^2 (95% CI: 5.0–25 ind./100 km^2) at Cágados (de Oliveira et al. 2020). The

Mel site is composed of dense, woodland savanna and has human settlements; whereas, at Cágados, the vegetation ranges from semiopen to dense, woodland savanna with no human presence. The difference in densities between both sites reflects the impact of human activity on the northern tiger-cat.

A major takeaway from these density studies is that the smaller species consistently occur at lower densities than the ocelot. This pattern has already been documented across the entire Neotropics using traditional capture–recapture models (de Oliveira et al. 2010). The SCR studies analyzed here show great variability in ocelot densities across the Neotropics and lower densities of margays and northern tiger-cats than those of ocelots (Fig. 3.4). SCR models are data-hungry and at least 20 recaptures are recommended for precise density estimates (Efford et al. 2009), which makes it difficult to apply them to small felids other than ocelots, given their rarity. The savanna tiger-cat density estimates, for example, were conducted at the species' main stronghold worldwide (de Oliveira et al. 2020). At sites in which ocelots attain densities higher than 10 ind./100 km^2, which would correspond to most lowland tropical forest habitats in the Neotropics, smaller felids are likely to be either absent or present at very low densities (de Oliveira et al. 2010, 2021a, b). Under these conditions, it is unlikely that we would be able to estimate small felid densities with high precision via SCR models. The margay densities from the Ecuadorean Amazon, for example, had to be conducted using an informative prior for the movement parameter based on a home-range study conducted in the Atlantic Forest (Gil-Sánchez et al. 2021; Kasper et al. 2016). This is because during the entire sampling period there was only one spatial recapture of margays (Gil-Sánchez et al. 2021). The resulting estimates were therefore less precise for margays than for ocelots: 22.25 ± 3.48 ind./100 km^2 for ocelots and 10.05 ± 7.77 ind./100 km^2 for margays at the Keweriono site, for example. Similarly, in Horn's study, margay densities could not be estimated at Turvo State Park due to the low number of records, which contrasted with a high amount of ocelot records (Horn et al. 2020).

3.6.2 Cormack–Jolly–Seber Model

The Cormack–Jolly–Seber (CJS) model is a probabilistic mark-recapture abundance model (Cormack 1964; Jolly 1965; Seber 1965). It estimates a capture (p) and survival (Φ) probability for an open population. This model has been applied to small Neotropical felids at two study sites in southeastern Mexico (Pérez-Irineo et al. 2017; Pérez-Irineo and Santos-Moreno 2016). In both studies, the authors derived abundance estimates for margays and ocelots by dividing the number of individuals recorded by the capture probability estimated from the CJS model. Afterward, densities were estimated by dividing the abundance by the effective sampled area (ESA), which was defined by a buffer that was equivalent to the mean maximum distance moved by the individuals around the camera-trap polygon. The two study sites were Los Chimalapas, part of the largest remaining tropical rainforest fragment in the Isthmus of Tehuantepec (Pérez-Irineo and Santos-Moreno 2016), and Sierra

Norte, a mountain range with semievergreen forest at lower elevations and cloud forests at higher elevations (Pérez-Irineo et al. 2017). At Los Chimalapas, estimated densities were 22 ind./100 km^2 (95% CI: 17–32 ind./100 km^2) for ocelots and 68 ind./100 km^2 (95% CI: 57–79 ind./100 km^2) for margays. At Sierra Norte, estimated densities for ocelots were 7.8 ind./100 km^2 and 81 ind./100 km^2 for margays, though with no confidence intervals given. The densities obtained for margays at both locations are much higher than any other estimate for a small Neotropical felid, other than the ocelot. Unfortunately, deriving abundance by dividing the number of individuals by the capture probability estimated from the CJS will inflate abundance whenever the capture probability is low. At Sierra Norte, for example, the authors detected 16 different individual margays, with a mean maximum distance moved (MMDM) of 1.9 km, an ESA of 63-km^{2,} and a capture probability of 0.30. Using only the number of individuals detected, the density would be 25 ind./100 km^2, which would still rank among the highest for the smaller felids (de Oliveira et al. 2020), but it is far smaller than the estimated 81 ind./100 km^2. Low capture probabilities stem from few recaptures of individuals and multiple detections of floaters (i.e., individuals detected only once during the whole study period). To avoid overestimating densities, we recommend designing the study to maximize spatial recaptures of the target species with camera spacing following known home ranges of the species in question (de Oliveira et al. 2020; Horn et al. 2020).

Comparatively, density estimates of classic mark-recapture methods of the small Neotropical species, although still limited, are far more common than those of SCR. The larger and dominant ocelot reaches significantly higher densities than the smaller species (<6 kg) (de Oliveira et al. 2010). The smaller species' known densities range from 0.1 to 25 ind./100 km^2 (Fig. 3.4) and are constrained by those of the ocelot (Fig. 3.5; range 3.1–94.7 ind./100 km^2) when above the threshold of 10–12 ocelots/100 km^2, which is known as the "ocelot effect" (de Oliveira et al. 2020, 2021a, b, in press).

3.7 Abundance Hierarchical Models

The Royle-Nichols model (RN) estimates occupancy probability when heterogeneity in detection probability occurs as a result of abundance variations (Royle and Nichols 2003). Given this relationship between detectability and abundance, the model theoretically could be used to derive site-abundance estimates. We found one instance in which this model has been applied to obtain an abundance estimate of small Neotropical felids (Penido 2016) and two in which the derived parameter λ was interpreted as occupancy with site-specific heterogeneity in detection (Stachowicz et al. 2021; Tobler et al. 2015).

At Serra da Capivara National Park, in the Brazilian Caatinga, the RN model was used to estimate the local abundance of ocelots and northern tiger-cats (Penido 2016) and explore changes in the abundance of both species between the two sampled

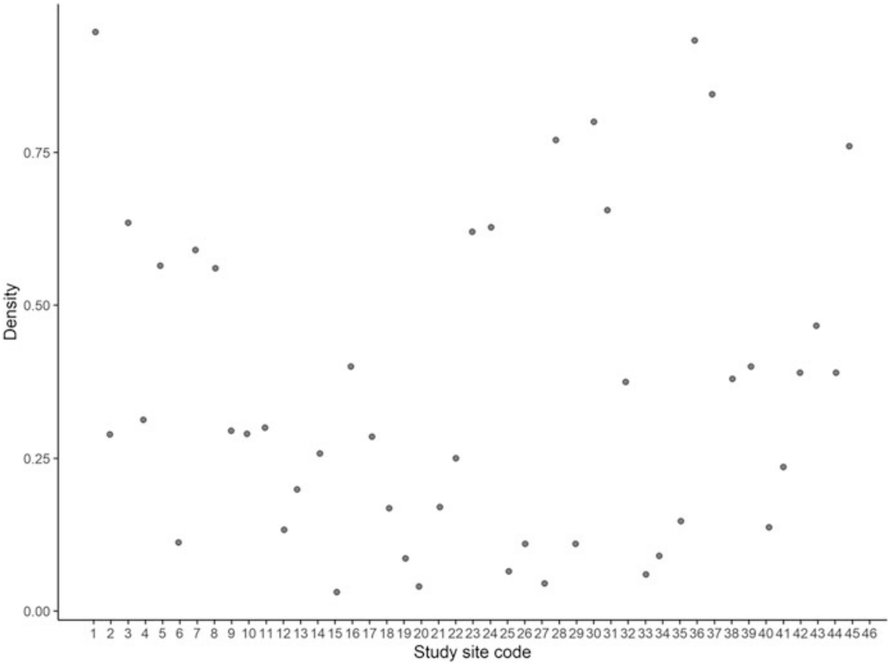

Fig. 3.5 Traditional capture–recapture model densities of ocelots at 45 study sites throughout the species' range (de Oliveira et al. 2022). The species consistently achieves densities above 0.25 ind./km^2 and reaches values of almost 1 ind./km^2 in the western Amazon. Study sites are as follows: 1. Block 39, Peruvian Amazon; 2. Amanhã Sustainable Reserve, Brazil; 3. Tiputini Research Station, Ecuador; 4. Morro do Diabo, Brazil; 5. UNIDERP, Brazil; 6. SESC, Pantanal, Brazil; 7. Ravelo, Bolivia; 8. San Miguelito, Bolivia; 9. Cerro Cortado, Bolivia; 10. Tucavaca, Bolivia; 11. Yturria Ranch, United States; 12. Uruguaí, Brazil; 13. Iguazu NP, Argentina; 14. Chiquibul National Park, Belize; 15. Mountain Pine Ridge, Belize; 16. Ilha do Cardoso, Brazil; 17. Feliciano Miguel Abdala Reserve, Brazil; 18. Iguazu NP and San Jorge Forest Reserve, Argentina; 19. Yaboti, Argentina; 20. Caraguatá, Brazil; 21. Ponte Branca, Brazil; 22. Seis R, Brazil; 23. Santa Monica, Brazil; 24. Darién NP, Panamá; 25. Talamanca Mountains, Costa Rica; 26. Palmarito Reserve, Colombia; 27. Serra da Capivara NP, Brazil; 28. Palmar, Bolivia; 29. Kaa Iya del Gran Chaco NP, Bolivia; 30. Cocha Cashu, Peru; 31. Turvo (Porto sector), Brazil; 32. Turvo (Salto sector), Brazil; 33. Sete Saloes, Brazil; 34. Laguna Atascosa National Wildlife Refuge, United States; 35. Mirador Río Azul Basin, Guatemala; 36. Lorocachi, Ecuador; 37. Maxus Road, Ecuador; 38. Los Chimalapas, México; 39. Hato Massaragual, Venezuela; 40. Iguaçu NP, Brazil; 41. Corcovado NP, Costa Rica; 42. Chamela-Cuixmala, México; 43. Medina, Colombia; 44. Rio Bravo Conservation Area, Belize; 45. Miranda Ranch

years (2009 and 2010). Abundance estimates in 2009 were 78.88 ± 9.28 for the ocelot and 42.34 ± 15.66 for the northern tiger-cat (corresponding to a density of 6.07 ± 0.71 ind./100 km^2 for the ocelot and 3.26 ± 1.2 ind./100 km^2 for the savanna tiger-cat); while, in 2010, abundance for both species declined, with 52.78 ± 9.86 individuals estimated for the ocelot and 33.06 ± 11.6 for the savanna tiger-cat (densities of 4.06 ± 0.76 ind./100 km^2 for ocelots and 2.54 ± 0.89 ind./100 km^2 for savanna tiger-cats). These density values were obtained by multiplying site-specific abundance estimates by the number of cameras and then them dividing by the total area of the park (Penido 2016); however, the author did not report site-specific abundance estimates. No covariates were used to model the abundance of either felid species for either year. As a comparison, ocelot density at the same park estimated through SCR models was 3.16 ± 0.46 ind./100 km^2 for the year 2009, which is roughly half of that obtained via RN for the same period (Penido et al. 2016).

Two studies used the RN to model the whole medium–large-sized mammal community of their respective study sites. In the Peruvian Amazon, the RN model was implemented in a multiseason framework to model species richness and occupancy (Tobler et al. 2015). The authors defined a categorical covariate to model variation in occupancy between *terra firme* forest and floodplains. For the detection parameter, the authors modeled the effect of on vs. off trail camera-trap location. A total of 289 detections of ocelots, 77 of margays, and 14 of jaguarundis were obtained in this study. Occupancy and detectability were higher for ocelots than for either margays or jaguarundis, regardless of habitat type or camera placement. Jaguarundis had in fact the fourth lowest occupancy value among all species sampled, only ahead of crab-eating raccoons, bush dogs, and greater grisons. In terms of effects on covariates, only ocelots showed a significant response, with higher occupancy in floodplains and higher detectability on trails (Tobler et al. 2015).

Finally, in Venezuela's Gran Sabana region, the authors applied the RN model to assess the effects of hunting on medium–large-sized mammals (Stachowicz et al. 2021). Of the small cats, ocelots were the only species with enough records to be included in the models, and the species showed no response to any of the covariates tested.

Because of the RN model's assumption of independent detections of individual animals at a camera site (Royle and Nichols 2003), this model is not practical for estimating the abundance of small felids. Resident individuals are likely to be detected at more than one camera site unless the intertrap spacing is greater than the movement parameter of the target species. Furthermore, it is not clear to what area the resulting abundance estimates refer to. This undefined, effectively sampled area is the key caveat point that undermines density estimates when using RN models. Even if a grid-cell size is defined a priori, cameras have a small detection zone, thus making it unreasonable to apply a site-abundance estimate to an arbitrarily wider area (Efford and Dawson 2012). Hence, for estimating the abundance of small Neotropical felids, we recommend designing a survey to analyze the data in an SCR (or other population capture–recapture) framework. Nevertheless, the RN model can be used to model occupancy whenever site-specific variation in detectability is suspected (Kéry and Royle 2015).

The issue with these models and the N-mixture models is that, in camera traps, we do not have counts as such, but frequency of records. However, given the spot patterns of these species, it would be possible to count "individuals," they are relative indices of abundance corrected for detection (Gilbert et al. 2021). In that sense, and given the characteristics of these species, capture–recapture models may be more useful. The caveat could be that unmarked species may need to use NR or N-mixtures.

3.8 Conclusions

This chapter sought to provide a review of tropical America's small felids abundance and occupancy patterns since this group as a whole remains poorly studied, and the vast majority of published works focus on ocelots. Given the grim conservation outlook regarding small cats, population monitoring, and density, estimates obtained through SCR models are vital. For instance, both tiger-cat species are globally threatened (de Oliveira et al. 2016; Payan and de Oliveira 2016). Additionally, caution needs to be taken in the approach used, even with SCR models, as some estimates might turn out highly inflated even when compared to those of nonspatial estimates or of highly abundant species. This, in turn, would be indeed detrimental to the conservation of the species. Furthermore, there are several geographic gaps in the coverage of HM studies in the Neotropics, with some countries being poorly represented or unrepresented in our sample (i.e., El Salvador, Honduras, Nicaragua, and Guyana). With increasing habitat loss across the Neotropics, as well as other threats (direct persecution, disease transmission, etc.), proper sampling that allows precise estimates of abundance, density, and occupancy is a major requirement for assessing conservation interventions for small felids in tropical America.

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Chapter 4
Tales from Southern Brazil: Hierarchical Modeling of Occupancy, Abundance, and Density of Atlantic Forest and Pampa Mammals

Flávia P. Tirelli, Cíntia da Costa, Marcelo G. Oliveira, and Maria João Ramos Pereira

Abstract This chapter provides an integrative overview of the occupancy and density of Neotropical mammals on the southern boundary of the Atlantic Forest and the Brazilian–Uruguayan Savanna. We demonstrate the application of different hierarchical modeling approaches to assess the impact of anthropogenic land-use changes on the occupancy, abundance, and density of fossorial, flying, and terrestrial mammals, specifically armadillos, bats, and carnivorans, particularly small cats. These analytical methods allowed us to draw ecological and conservation conclusions for each of the groups studied. Our results show that land-use changes have different effects on the occupancy and density of the different species studied. Overall, our results provide valuable insights into the ecology and conservation of Neotropical mammals in human-dominated landscapes. In the future, several research directions can be pursued, including investigating the mechanisms underlying the differential impacts of anthropogenic landscape changes and disturbance, as well as the ecological and conservation requirements of different mammal species.

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4.1 Introduction

The spatial arrangement of habitats influences the ecological processes that affect animal movement patterns in habitat selection, survival, and dispersal (Dunning et al. 1992; Royle et al. 2014). Understanding species distribution and spatial variation, including site occupancy patterns, is key to developing wildlife conservation and management programs (Bennett et al. 2009). Occupancy and density modeling are fundamental approaches in studies of wildlife population ecology (Royle et al. 2014; Mackenzie et al. 2018). Occurrence metrics support inferences about habitat relationships, species distribution, disease dynamics, metapopulation dynamics, paleobiology, and large-scale monitoring (Mackenzie et al. 2018). Species occupancy and/or abundance can be modeled using habitat or landscape features as predictors. Such models are often based on the presence or absence of a species at a particular sampling site, or rather its detection or nondetection, while simultaneously measuring habitat or landscape features of potential biological interest at the same sampling sites (Mackenzie et al. 2018). Population densities can be estimated using Spatial Capture–Recapture (SCR) models, based on individual encounter history data linked to capture location information. Such models necessarily depend on unique individual identifications. In addition, these models allow the assessment of parameters such as space use, movement patterns, spatial organization of individuals, density variation, and resource selection. All these spatial processes are influenced by the spatial arrangement of the habitat, which is a key element, especially in ecotones. Ecotones are transitional areas between ecological ecosystems, communities, or ecological regions along an environmental gradient. Many studies have shown that species richness and abundance tend to be greatest in ecotone regions (Kark 2013). Therefore, knowledge of the abovementioned spatial processes in wildlife populations that occur in these megadiverse transition areas is crucial for Ecology and Conservation.

The state of Rio Grande do Sul (RS) in the extreme south of Brazil lies on the border between the Atlantic Forest and the Uruguayan Savanna domains. The Brazilian part of the Uruguayan Savanna is known as the Brazilian Pampa. This transitional region is unique because the differences in the physiognomy of the two areas are striking. The Atlantic Forest includes a variety of forest physiognomies and ecoregions, including Semideciduous, Deciduous Stationary, and Ombrophylus cloud forests (Araucaria forest) (Marques and Grelle 2021), which have high levels of floristic and faunal endemism. The Pampa is characterized by extensive grasslands and shrublands with some riparian forests (Boldrini 2009). The ecotone between the Atlantic Forest and the Pampa therefore represents the southern range limit of forest specialists and the northern range limit of grassland specialists, creating a hotspot of diversity, especially for mammals.

There are about 175 mammal species in the region, representing about 25% of the mammals in Brazil (Weber et al. 2013). Rio Grande do Sul is the Brazilian state with the greatest diversity of felids (Carnivora: Felidae), with eight of the ten Brazilian cats occurring in this area (Espinosa et al. 2018; Nagy-Reis et al. 2019; Tirelli et al. 2021). Other mammal taxa are also diverse: 42 species of bats (Chiroptera) occur in the state (Noronha 2016), including two with restricted ranges: *Myotis pampa* (Novaes et al. 2021) and *Eumops patagonicus* (Bernardi et al. 2009); and four armadillo species (Cingulata, Xenarthra) of the 11 found in Brazil: *Cabassous tatouay*, *Dasypus novemcinctus*, *Dasypus septemcinctus*, and *Euphractus sexcinctu*s (Santos et al. 2019).

Due to widespread conversion to agricultural, forestry, and urban landscapes, the Atlantic Forest and the Pampa are currently restricted to small fragments in a matrix of human-dominated landscapes (Marques and Grelle 2021; Overbeck et al. 2015). From 1985 to 2020, the state of Rio Grande do Sul has lost 10% of the natural areas of the Atlantic Forest and 21% of the natural areas of the Pampa (Souza et al. 2020). In such a scenario, native mammals face the challenge of adapting to different and rapidly changing conditions, taking into account both extrinsic anthropogenic factors and intrinsic factors at the species level, encompassing biological, ecological, and evolutionary domains. In this chapter, we present the approaches and main results of recent studies conducted by our team based on noninvasive monitoring schemes, especially using camera traps and ultrasound detectors. Overall, we have investigated the environmental factors affecting site occupancy, abundance, and density of three mammal groups in Rio Grande do Sul, Brazil (Fig. 4.1). Our aim

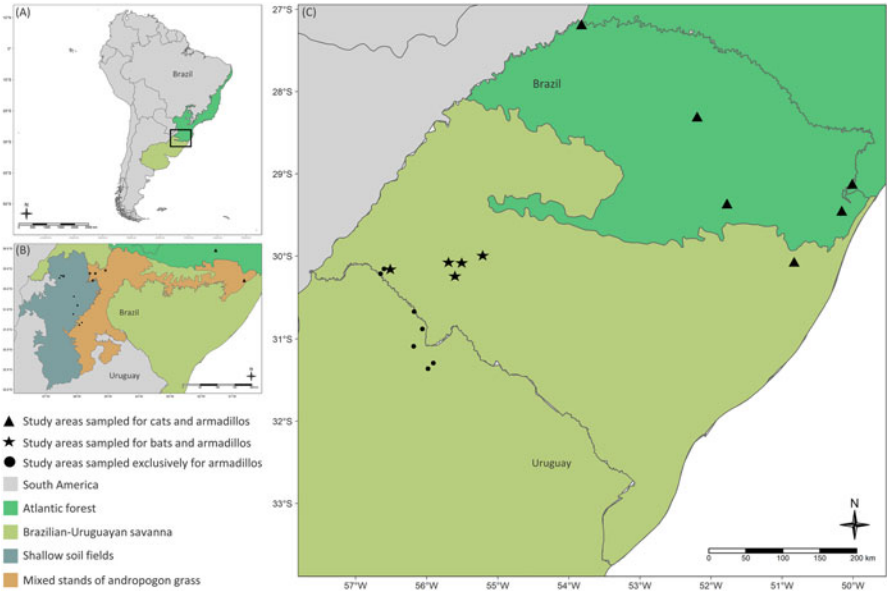
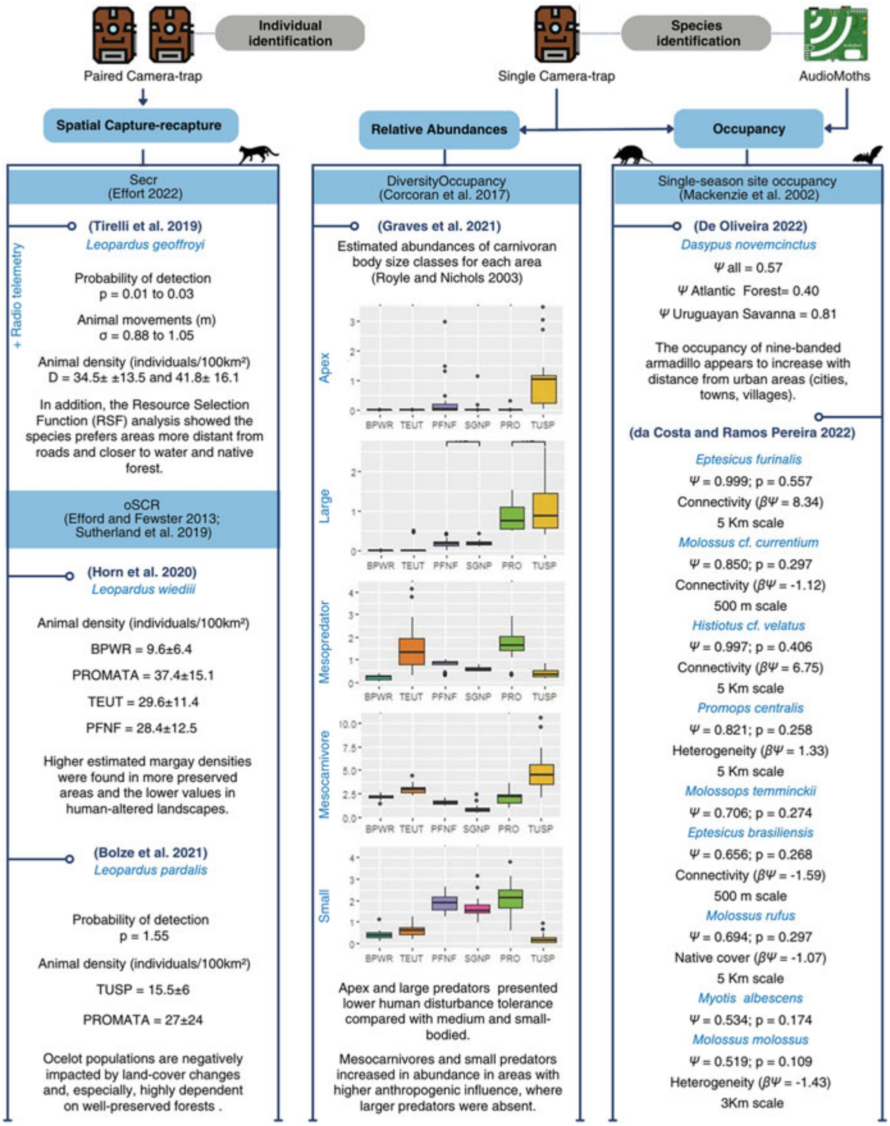


Fig. 4.1 (**a**) Location of the Brazilian–Uruguayan Savanna ecoregion and southernmost Atlantic Forest in Brazil, within South America in light gray. (**b**) The two main physiognomies occurring in the Brazilian and Uruguayan grasslands: in turquoise the shallow soil fields and in orange the mixed stands of andropogon grass. (**c**) Location of the 18 areas in the Brazilian Pampa and the southernmost Atlantic Forest, sampled for bat, armadillos, and cats by acoustic and camera-trap monitoring between 2015 and 2021

is to demonstrate the use of different hierarchical modeling approaches in assessing the impacts of anthropogenic land-use change on wildlife, using fossorial, flying, and terrestrial mammals, respectively, armadillos (de Oliveira 2022), bats (da Costa and Ramos Pereira 2022), and carnivorans (Graves et al. 2021), including wild cats (Tirelli et al. 2019; Horn et al. 2020; Bolze et al. 2021), as models (Fig. 4.2).



(Tirelli et al. 2019)
Leopardus geoffroyi

Probability of detection
p = 0.01 to 0.03

Animal movements (m)
σ = 0.88 to 1.05

Animal density (individuals/100km²)
D = 34.5± ±13.5 and 41.8± 16.1

In addition, the Resource Selection Function (RSF) analysis showed the species prefers areas more distant from roads and closer to water and native forest.

(Horn et al. 2020)
Leopardus wiedii

Animal density (individuals/100km²)
BPWR = 9.6±6.4
PROMATA = 37.4±15.1
TEUT = 29.6±11.4
PFNF = 28.4±12.5

Higher estimated margay densities were found in more preserved areas and the lower values in human-altered landscapes.

(Bolze et al. 2021)
Leopardus pardalis

Probability of detection
p = 1.55

Animal density (individuals/100km²)
TUSP = 15.5±6
PROMATA = 27±24

Ocelot populations are negatively impacted by land-cover changes and, especially, highly dependent on well-preserved forests .

(Graves et al. 2021)

Estimated abundances of carnivoran body size classes for each area (Royle and Nichols 2003)

Apex and large predators presented lower human disturbance tolerance compared with medium and small-bodied.

Mesocarnivores and small predators increased in abundance in areas with higher anthropogenic influence, where larger predators were absent.

(De Oliveira 2022)
Dasypus novemcinctus

Ψ all = 0.57
Ψ Atlantic Forest= 0.40
Ψ Uruguayan Savanna = 0.81

The occupancy of nine-banded armadillo appears to increase with distance from urban areas (cities, towns, villages).

(da Costa and Ramos Pereira 2022)

Eptesicus furinalis
Ψ = 0.999; p = 0.557
Connectivity (βΨ = 8.34)
5 Km scale
Molossus cf. currentium
Ψ = 0.850; p = 0.297
Connectivity (βΨ = -1.12)
500 m scale
Histiotus cf. velatus
Ψ = 0.997; p = 0.406
Connectivity (βΨ = 6.75)
5 Km scale
Promops centralis
Ψ = 0.821; p = 0.258
Heterogeneity (βΨ = 1.33)
5 Km scale
Molossops temminckii
Ψ = 0.706; p = 0.274
Eptesicus brasiliensis
Ψ = 0.656; p = 0.268
Connectivity (βΨ = -1.59)
500 m scale
Molossus rufus
Ψ = 0.694; p = 0.297
Native cover (βΨ = -1.07)
5 Km scale
Myotis albescens
Ψ = 0.534; p = 0.174
Molossus molossus
Ψ = 0.519; p = 0.109
Heterogeneity (βΨ = -1.43)
3Km scale

Fig. 4.2 General summary scheme of the main results of the studies discussed in this chapter on the occupancy and density of Neotropical mammals, including armadillos, aerial insectivorous bats, and small cats in the southern limit of the Atlantic Forest and the Brazilian Pampa, developed from noninvasive approaches. Abbreviations: SGNP (Serra Geral National Park); BPWR (Banhado dos Pachecos Wildlife Refuge); PROMATA (Pro-Mata Center for Research and Conservation of Nature); TUSP (Turvo State Park); TEUT (Teutônia); PFNF (Passo Fundo National Forest)

4.2 Modeling Species Occupancy in Response to Landscape Structure in Armadillos and Bats

Monitoring fossorial and flying animals is a challenge for research, especially in megadiverse regions such as the Neotropic. Armadillos are fossorial and spend much of their time underground (Aguiar and Fonseca 2008), while bats, especially from the aerial insectivore guild, spend most of their active time flying at high altitudes (Denzinger and Schnitzler 2013). Apart from the difficulties in detecting those animals under our feet or above our heads, many armadillo species and all but very few bats are predominantly nocturnal. Such traits prevent the use of conventional sampling methods and make it difficult to evaluate population parameters. Especially in the Neotropic, where all armadillos and a large number of insectivorous bats are endemic, most ecological aspects of many, if not most, species are almost completely unknown (Superina et al. 2013; Bernard et al. 2011). Due to the limitations of conventional sampling methods and the wide range of many species, we are faced with a glaring Wallacean shortfall (Lomolino 2004) for armadillos and aerial insectivorous bats in the Neotropic.

Single-season site occupancy analyses are an efficient way to decipher the relationship between habitat characteristics and the occurrence of species in those groups. Using camera traps for armadillos and acoustic monitoring for bats, researchers can passively collect large amounts of data over long periods of time and large areas. The data obtained take the form of detection (1) and nondetection (0) histories, which allows the construction of hierarchical occupancy models that account for imperfect detection (MacKenzie et al. 2002). In this way, it is possible to estimate, with minimal bias, the probability of a site being occupied (ψ) by a species as well as the probability of detecting (p) the species in each site, provided that it occurs in the region and specifically at that particular site. Hierarchical occupancy models also allow for the addition of various (independent) covariates that may include aspects of local and regional landscape structure (Heim et al. 2015; Smith et al. 2021) and climate (Bailey et al. 2017). Next, we present two studies focusing on single-season site occupancy models for armadillos (de Oliveira 2022) and insectivorous bats (da Costa and Ramos Pereira 2022) in different areas of the Atlantic Forest and Pampa domains.

4.2.1 Site Occupancy by Armadillos in the Southern Atlantic Forest and the Uruguayan Savanna

To date, four armadillo species are recognized as occurring in southern Brazil and Uruguay: the greater naked-tailed armadillo (*Cabassous tatouay*), the nine-banded armadillo (*Dasypus novemcinctus*), the seven-banded armadillo (*D. septemcinctus*), and the six-banded armadillo (*Euphractus sexcinctus*) (Santos et al. 2019). As with all armadillos, there is a significant knowledge gap for these species (Superina et al.

2013). From a conservation perspective, this poses a serious problem, as even defining the conservation status of the species becomes unattainable; indeed, *C. tatouay* and the southern population of *D. septemcinctus* in Brazil are currently categorized as data deficient in Brazil (ICMBio 2015). Furthermore, these species and *D. novemcinctus* are considered threatened with extinction in Uruguay (Soutullo et al. 2013). In an effort to expand the limited knowledge of armadillo ecology in this region, we sought to estimate site occupancy probabilities (Ψ) of the species occurring here.

We sampled five areas in the Atlantic Forest of southern Brazil and 13 in the Uruguayan Savanna: eight in the Brazilian part and five in the Uruguayan part. We set up to 20 camera traps in each area (each site at a distance of at least 1 km), 162 sites in total, and left them for 60 days in spring and summer. We fitted the camera-trap data to single-species single-season site occupancy models (Mackenzie et al. 2002), which included various combinations of covariates that we hypothesized would influence armadillo occupancy probabilities (Ψ). We selected plausible models based on the Akaike Information Criterion (Burnham and Anderson 2004) and averaged multiple plausible models. This was done using the R version 4.0.2 (R Core Team 2021), "unmarked" version 1.1.1 (Fiske and Chandler 2011), and AICcmodavg version 2.3-1 (Mazerolle 2006). To determine whether armadillo site occupancy patterns vary between and within the two domains, we repeated the analyses for three datasets: (i) all data, (ii) Atlantic Forest data, and (iii) Uruguayan Savanna data.

We obtained 618 independent records of *D. novemcinctus*, 26 of *E. sexcinctus*, 25 of *D. septemcinctus*, and 15 of *C. tatouay*. We were able to generate adequate models only for *D. novemcinctus*, due to the low number of detections for the remaining three species. Modeling for all data resulted in six plausible models, with an average mean Ψ of 0.57, showing a statistically significant effect ($p < 0.05$) for one site occupancy covariate. By our predictions, the "distance to urban areas" covariate correlated positively with Ψ (Fig. 4.3). We obtained another six plausible models for the Atlantic Forest and the Uruguayan Savanna datasets, with estimated means Ψ of 0.40 and 0.81, respectively, after being averaged. The average models did not show statistically significant covariate effects on Ψ.

Since the ecology of armadillos in this region has been little studied, we find it difficult to explain the discrepancy between the number of records of *D. novemcinctus* and the other species. We now want to investigate whether there is indeed a difference in the abundance of armadillos, or whether the sampling method is unsuitable for some species. We have found that the occupancy of *D. novemcinctus* appears to increase with distance from urban areas (cities, towns, villages), which makes sense considering that the species is also negatively affected in other ways by proximity to humans (DeGregorio et al. 2021). The difference between the estimated mean Ψ-values for the Atlantic Forest and the Uruguayan Savanna may be explained by the overall shorter distances to the nearest urban areas that the sampled sites in the Atlantic Forest have. The values of this covariate varied much less within each dataset than between them, which explains why it is not significant in the respective occupancy models

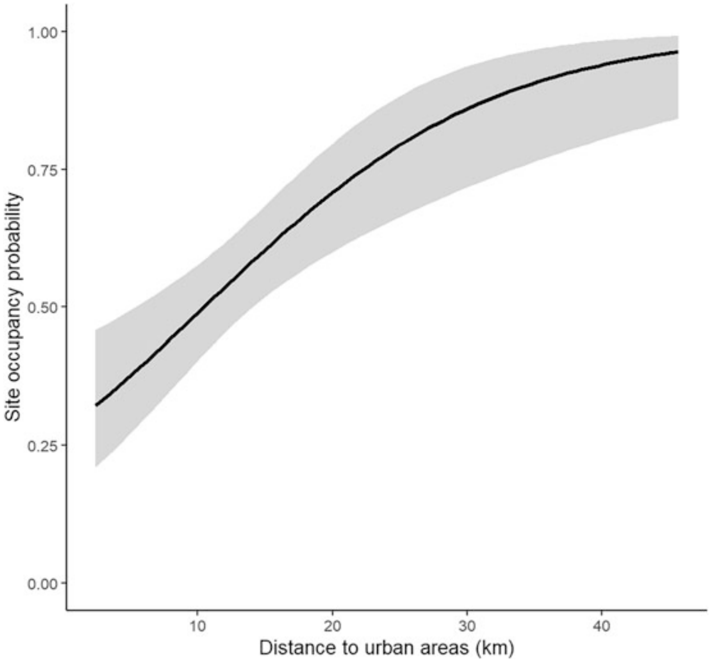


Fig. 4.3 Correlation between *Dasypus novemcinctus* site occupancy probability (Ψ) and the distance to urban areas in all sampled sites (dataset *i*). Dots represent detection (1) and nondetection (0) data for each site

4.2.2 Occupancy by Aerial Insectivorous Bats in the Brazilian–Uruguayan Savanna Evaluated Through Acoustic Detection

The Pampa represents the second least studied area for bats in Brazil (Bernard et al. 2011; Aguiar et al. 2020). Previous studies using mist nets and active roost search showed that most bats in the Pampa are aerial insectivores, either open-space or edge-space foragers (Noronha 2016). However, because of their specialized echolocation, which allows them to detect tiny prey, and because they fly relatively high, insectivorous bats are rarely captured by mist nets. Roost search is also more efficient when underground or human-made roosts are abundant, resulting in high quality data for inventories, species density and roost ecology studies, but not necessarily for habitat or landscape use studies by the species present in these roosts. The most appropriate and efficient method for aerial detection of insectivorous bats, especially in open environments, is therefore acoustic monitoring (Kalko et al. 2008).

In da Costa and Ramos Pereira (2022), we acoustically monitored 68 sites classified into one of the two main physiognomies (shallow soil fields and mixed stands of andropogon grass), to model the occupancy of aerial insectivorous bats in response to landscape structure at different scales, considering the influence of temperature and relative humidity on bat detection. Using the "landscapemetrics" package (Hesselbarth et al. 2019) in R Program version 4.0.4 (R Core Team 2021) we extracted metrics of connectivity, heterogeneity, and percentage of native vegetation cover in the landscape, from a categorical land-use raster of the Brazilian Pampa (MapBiomas Pampa Sudamericano Project 2021). All metrics were calculated for seven circular buffers (500 m, 1.0 km, 1.5 km, 2.0 km, 3.0 km, 4.0 km, and 5.0 km radius). We detected bat passes in 8111 (8.15%) out of 99,526 recordings and identified at least 11 species of the Molossidae and the Vespertilionidae: *Molossus* cf. *currentium*, *Molossus molossus*, *Molossus rufus*, *Promops centralis*, *Molossops temminckii*, *Eptesicus brasiliensis*, *Eptesicus furinalis*, *Histiotus* cf. *velatus*, *Myotis albescens*, *Myotis ruber*, and *Lasiurus blosevillii*. We likely detected other species, but because some echolocation call parameters overlap between some species, those were categorized as species or genera complexes (for a review of echolocation calls of Brazilian bats see Arias-Aguilar et al. 2018). We highlight the records of *Promops centralis* and *Molossus* cf. *currentium* as new occurrences for the region, expanding their distribution limits.

Occupancy probability was modeled using mean temperature and mean relative humidity as detection covariates (p) and the landscape metrics mentioned above as occupancy covariates (Ψ) at each of the seven scales analyzed, resulting in a total of four models for detection and 21 models for occupancy for 9 of the 11 species detected (*Lasiurus blosevillii* and *Myotis ruber* were excluded from occupancy modeling because they accounted for less than 1% of the total bat passes). We fitted all models using the occu function in the "unmarked" R package (Fiske and Chandler 2011) and considered the best-supported models those with ΔAICc $<$ 2 (Burnham and Anderson 2002).

Our results indicate that different bat species perceive the landscape differently, regardless of whether they use edge or open spaces. Occupancy probabilities of *Eptesicus brasiliensis* and *Molossus* cf. *currentium* increased with landscape connectivity at the 500 m scale, whereas occupancy probabilities of *Eptesicus furinalis* and *Histiotus* cf. *velatus* at the 5.0 km scale were negatively affected by landscape connectivity. *Molossus molossus* occupancy probability responded negatively to landscape heterogeneity at the 3.0 km scale, whereas *Promops centralis* occupancy probability responded positively to landscape heterogeneity at the 5.0 km scale. The occupancy probability of *Molossus rufus* responded negatively to native vegetation cover and positively to landscape heterogeneity at the 5.0 km scale. Occupancy probabilities of *Myotis albescens* and *Molossops temminckii* did not respond significantly to any of the landscape metrics evaluated.

To spatially extrapolate our results, we used the "modavgPred" function in the R package AICcmodavg (Mazerolle 2020). We combined a categorical land-use raster (MapBiomas Pampa Sudamericano Project 2021) with the shapefile adapted from the two phytophysiognomies studied, covering areas of the Uruguayan Savanna in Brazil and in the bordering Uruguay. We created a grid over the polygon and extracted the coordinates of each cell and the landscape metrics used as occupancy covariates in the hierarchical models to create a new data frame. Using this information, we created maps of projected occupancy for each species in the region (Fig. 4.4) using the "raster" (Hijmans 2012), "rgdal" (Bivand et al. 2015), "sp"

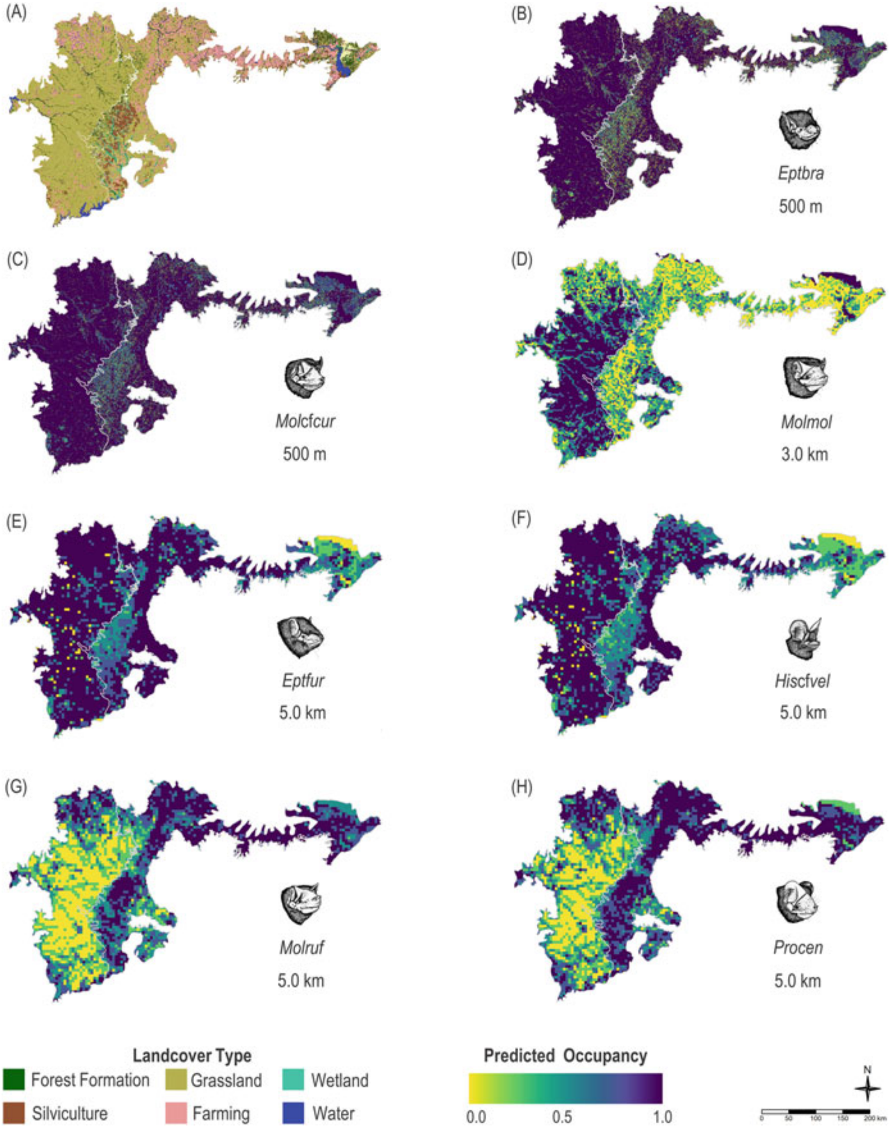


Fig. 4.4 Estimated occupancy for nine species of bats for the area occupied by two main phytophysiognomies present in the Brazilian and Uruguayan portion of the Uruguayan Savanna – shallow soil fields and mixed stands of andropogon grass, based on the modeling results using the bat acoustic data gathered in the Brazilian Pampa during spring and summer 2019 and 2020: (**a**) map showing land-cover types, (**b**) *Eptesicus brasiliensis* (*Eptbra*), (**c**) *Molossus* cf. *currentium* (*Mol*cf*cur*), (**d**) *Molossus molossus* (*Molmol*), (**e**) *Eptesicus furinalis* (*Eptfur*), (**f**) *Histiotus* cf. *velatus* (*His*cf*vel*), (**g**) *Molossus rufus* (*Molruf*), (**h**) *Promops centralis* (*Procen*). (Modified from da Costa and Ramos Pereira (2022))

(Pebesma and Bivand 2005), and "tmap-R" packages (Tennekes 2018). Our projected occupancy estimates for the phytophysiognomies studied ranged from 0.45 to 0.70 for all bat taxa. The estimated occupancy of open-space foragers *Molossus rufus* and *Promops centralis* was associated with heterogeneous landscape elements and showed some tolerance to modified landscape matrices. On the other hand, landscapes where native elements, especially the espinilho tree (*Acacia caven*), wetlands, water, and riparian forests, are preserved seem to favor the occupancy of the edge-space foragers *Histiotus* cf. *velatus*, *Eptesicus brasiliensis*, *Eptesicus furinalis*, and the open-space forager *Molossus* cf. *currentium*. The open-space forager *Molossus molossus*, a fairly common species in the region, appears to prefer native grasslands interspersed with native forest formations and small- and medium-sized water bodies. Areas of excessive forest management and agriculture do not appear to favor any of the bats recorded. Rapid anthropogenic changes in the Pampean landscapes, primarily due to intensive livestock production on natural grasslands and conversion of native grasslands to intensive forestry and agricultural plantations, with only 46% of natural vegetation remaining, undoubtedly affect not only bats, which are quite vagile, but also other animal groups, particularly those with lower dispersal abilities and greater resource dependence.

4.3 Defaunation in the Southern Limit of the Atlantic Forest: Abundance Modeling for Carnivorans of Different Sizes

There are three recognizable phases in defaunation (Young et al. 2016): (1) low-tech small-scale hunting depletes megafauna; (2) the adoption of more sophisticated hunting techniques leads to additional declines in the megafauna; and (3) further exploitation and anthropogenic landscape changes lead to significant population declines and, eventually, extinctions. The level of defaunation of a given region depends on the resilience of each species in the regional pool. Species resilience is a result of extrinsic (including the predictability of environmental changes, level of habitat fragmentation, and depletion) and intrinsic factors, such as life-history and biological and ecological traits. Some species may persist in anthropogenically modified areas, or even benefit from additional foraging or roosting resources made available in these areas (Di Bitetti et al. 2010). Some of these "heroes of the resistance" include generalists or scavengers, often displaying avoidance behaviors to reduce encounters with either humans or with potential predators or superior competitors (Monterroso et al. 2020). Other species, on the other hand, are quite demanding in terms of habitat quality. In mammals, and carnivorans (Carnivora, Mammalia) in particular, the body size is a good indicator of extinction susceptibility (Lino et al. 2019; Wolf and Ripple 2017): simply put, larger species tend to require larger home ranges and, usually, larger prey, thus being under increased extinction risk from habitat fragmentation and destruction than smaller carnivorans, which may present higher abundances in disturbed areas due to increased tolerance combined with competitive release from the depletion or extinction of the larger fauna (Wearn et al. 2017).

In Graves et al. (2021), using camera-trap data from six areas of the austral Atlantic Forest in Brazil, we evaluated the responses of carnivorans of different body sizes to anthropogenic landscape changes and disturbance. The six sites were chosen to reflect variation in those conditions. The 12 species detected were divided into five groups based on body size and carnivory level: (i) apex predators (hypercarnivores $>$ 60 kg; only the jaguar *Panthera onca*), (ii) large predators (hypercarnivores 10–60 kg; puma *Puma concolor* and ocelot *Leopardus pardalis*), (iii) mesopredators (hypercarnivores 3–10 kg; margay *Leopardus wiedii* and jaguarundi *Herpairulus yagouaroundi*), (iv) mesocarnivores (omnivores of 3–10 kg; pampas fox *Lycalopex gymnocercus*, crab-eating fox *Cerdocyon thous*, tayra *Eira barbara*, coati *Nasua nasua* and crab-eating raccoon *Procyon cancrivorus*), (v) and small predators (hypercarnivores $<$ 3 kg; southern oncilla *Leopardus guttulus* and lesser grison *Galictis cuja*).

Using the “DiversityOccupancy” package v1.0.6 (Corcoran et al. 2017) for R v3.4.4 (R Core Team 2018), we fitted occupancy models for species abundances (Royle and Nichols 2003) with automatic model selection, using as covariates stable light at night and distance to nearest phone tower (Macedo et al. 2018) as proxies for human activity and presence within the sites, and area of connected forest and distance to forest edge as measures of habitat fragmentation for each site. Distance to the closest protected area was also included to assess the importance of protected areas to the carnivoran assemblage of the region. The occupancy of potential mammalian prey and domestic carnivores (cat *Felis catus* and dog *Canis familiaris*) were modeled with detection data obtained simultaneously in the same sites and were subsequently included as covariates in the carnivoran abundance occupancy models.

In Table 4.1, we present the best-fit model for each predator size group. Apex and large predators presented lower tolerance to human disturbance compared with medium- and small-bodied carnivores. Indeed, apex carnivorans were only detected at the one site considered as being in the second phase of defaunation with hunting as the primary anthropogenic threat, whereas all the remaining are already in the third phase (no site could be considered as being in the first phase). Large predators also showed increased abundance in the same second-phase defaunation site. Mesocarnivores and small predators increased in abundance in areas with higher anthropogenic influence, where the larger predators were largely absent, suggesting mesopredator release. Still, multiple species were either absent or presented low predicted abundances in the site showing the greatest levels of anthropogenic landscape change and disturbance, evident from high stable light at night values and low distance to cell phone towers. This suggests the existence of a threshold of anthropogenic disturbance affecting even the “heroes of the resistance,” in this context, the small-bodied carnivores. These results lead us to put forward the idea of a novel ecosystem form of mesopredator suppression, with humans as the apex predator creating a landscape of fear.

Table 4.1 Best-fit model for predator size groups with model formula, AIC and estimate, standard error (SE), *z*-statistic, and *P* for each parameter

Predator group	Formula	Type	Parameter	Estimate	SE	*z*	*P*
Apex	~Distance ~ACF +Domestic +L +Light +S +XL	Detection	(Intercept)	−26.000	822.000	−0.032	>0.05
			Distance	20.000	745.000	0.027	>0.05
		Abundance	(Intercept)	−12.813	77.418	−0.166	>0.05
			ACF	−4.911	7.100	−0.692	>0.05
			Domestic	0.584	0.326	1.791	>0.05
			L	3.654	1.936	1.888	>0.05
			Light	−13.604	127.212	−0.107	>0.05
			S	−5.131	1.978	−2.594	0.009**
			XL	−2.587	1.081	−2.393	0.017*
Large	~Distance +TC ~L +Light +Phone	Detection	(Intercept)	−2.260	0.300	−7.530	<0.001
			Distance	0.619	0.199	3.120	0.001**
			TC	0.404	0.115	3.520	<0.001***
		Abundance	(Intercept)	−4.950	11.204	−0.442	>0.05
			L	0.594	0.236	2.511	0.012*
			Light	−6.373	18.449	−0.345	>0.05
			Phone	0.569	0.177	3.214	0.001**
Mesopredator	~TC ~ACF +Light +Phone	Detection	(Intercept)	−3.127	0.377	−8.290	<0.001
			TC	0.658	0.128	5.150	<0.001***
		Abundance	(Intercept)	−0.538	0.348	−1.550	>0.05
			ACF	0.647	0.147	4.400	0.001**
			Light	−0.694	0.245	−2.830	0.005**
			Phone	−0.476	0.216	−2.200	0.028*
Mesocarnivore	~TC +Time ~Edge +L +S	Detection	(Intercept)	−1.625	0.152	−10.690	<0.001
			TC	1.160	0.104	11.170	<0.001***
			Tempo	−0.305	0.107	−2.840	0.004**
		Abundance	(Intercept)	0.772	0.139	5.570	2.50E-08

			Edge	0.293	0.066	4.420	<0.001***
			L	0.202	0.086	2.360	0.018*
			S	−0.384	0.101	−3.810	<0.001***
Small	~TC ~Edge +L +Light +XL	Detection	(Intercept)	−3.173	0.348	−9.110	<0.001
			TC	0.776	0.179	4.330	<0.001***
		Abundance	(Intercept)	−0.460	0.338	−1.360	>0.05
			Edge	−0.492	0.257	−1.920	>0.05
			L	0.489	0.193	2.530	0.011*
			Light	−0.344	0.223	−1.550	>0.05
			XL	−1.158	0.326	−3.550	0.003***

Modified from Graves et al. (2021)

The detection model parameters are the activation distance of the camera sensor (Distance), activation time of the camera sensor (Time), and total count of records (TC). Occupancy model parameters are an area of connected forest (ACF), distance to forest edge (Edge), distance to cell phone tower (Phone), stable light at night values (Light) along with modeled abundances of domestic carnivores (Domestic), mega (XL), large (L), and small (S) mammalian prey species. Significance levels shown represent <0.05*, <0.01**, and <0.001***

4.4 Counting Cats: Factors Affecting Population Densities of Small Neotropical Felids

Reliable population density data are essential for determining appropriate wildlife conservation strategies (Royle et al. 2014). In addition to density estimates (D), other population parameters are important, such as probability of detection (p) and animal movements (σ). Camera traps are commonly used to detect and individually identify mammals with unique fur patterns such as spots, stripes, or rosettes, which are particularly common in many wild cats (Royle et al. 2014). By combining the detection history of individuals (identified by their unique fur patterns as recorded in camera traps) with activation history and location of camera traps (which may include temporal and/or spatial variables), it is possible to create SCR models to test various hypotheses. Spatial Capture–Recapture (SCR) models use the spatial information of the detector and assume that its location influences the likelihood of detecting an individual (Royle et al. 2014). Below, we present the relevant approaches and results of three studies in which we used SCR models to estimate densities of (i) Geoffroy's cats (*L. geoffroyi*) (Tirelli et al. 2019), (ii) margays (*L. wiedii*) (Horn et al. 2020), and (iii) ocelots (*Leopardus pardalis*) (Bolze et al. 2021). The first study took place in the Brazilian part of the Uruguayan Savanna and the last two in the southern limit of the Brazilian Atlantic Forest.

4.4.1 Density and Space Use by Geoffroy's Cats in a Human-Dominated Pampean Landscape

The Geoffroy's cat (*Leopardus geoffroyi*) is a solitary small wild cat distributed from Bolivia and southernmost Brazil to the southern tip of South America (Macdonald and Loveridge 2010; Cuyckens et al. 2016). This species is classified as Least Concern by the IUCN (Pereira et al. 2015). Previous studies suggested that the Geoffroy's cat is an ecologically adaptable species (Castillo et al. 2008; Pereira et al. 2012, 2015; Caruso et al. 2016), as it appears to have some tolerance for habitat change, with populations persisting alongside livestock and agriculture. With this in mind, we aimed to estimate population densities and characterize habitat preferences of Geoffroy's cats in a human-dominated landscape.

The study by Tirelli et al. (2019) was conducted on two contiguous private ranches in the Brazilian portion of the Uruguayan Savanna. The study area consisted of a mosaic of natural habitat remnants, cattle pastures, and cropland surrounding the Arroio Caverá River. We used camera traps and data from VHF telemetry to estimate the density of the Geoffroy's cat population and to determine the habitat preferences of the species in the region. The camera trap consisted of 13 stations with paired cameras. The distance between each pair of stations was approximately 600 m, which is the radius of the smallest home-range recorded for this species (Pereira et al. 2012). During the same period, we also captured adult Geoffroy's cats and fitted them with VHF radio collars equipped with activity and mortality sensors (Telonics – MOD-080-2), following the recommendations of the American Society of Mammalogists (Sikes 2016). Live capture and handling were performed under permit SISBIO-36803 and approved by the Pontifícia Universidade Católica do Rio Grande do Sul Ethics Committee for Animal Welfare and Use (PUCRS CEUA – 14/00400).

We estimated Geoffroy's cat density in summer (January and February 2015) and in winter (end of June to the beginning of August 2015). Both periods were limited to 48 days to meet the assumption of population closure (Balme et al. 2009). After individual identification, density was estimated with SECR models (Royle et al. 2014), using the package "secr" (Efford 2018) in R software. In this study, we did an innovative analysis combining different types of data: camera-trapping records with animal locations obtained by radio telemetry. We only included the telemetry data from individuals that were monitored during the survey periods delimited by the camera-trap sampling. We created six different models including combinations of sex, age, and particular behavioral features to represent capture history, and tested their relative performances using the Akaike Information Criterion (AIC) (Akaike 1974). In addition to density, we calculated resource selection functions (RSF). These analyses were based on the locations of individuals obtained via telemetry and spatial variables, such as habitat composition, distance to roads, and distance to water. These variables were chosen because water is a crucial resource, and the mosaic of habitat composition and roads are the main features of the study area. We then created nine distinct models including different combinations of the variables using General Linear Models (GLM) in package "lme" 41.1–17 (Bates et al. 2015) in R software. After that, we compared the models using the AIC, and from our top model, we created a map of predicted habitat suitability using the package "adehabitatHS" (Calenge 2011).

We live-captured 12 Geoffroy's cat individuals, seven of which (four males and three females) were radio-collared and monitored. In the summer survey, from 49 independent camera-trap captures, we identified 11 different Geoffroy's cat individuals (four males and seven females). For five of them (three males and two females), we obtained telemetry data (37 total points) that were incorporated into the combined density estimates. In the winter survey, from 33 independent camera-trap captures we recognized 11 distinct individuals (five males and six females). Nine individuals (three males and six females) overlapped with those identified in the summer. In this case, we could only include telemetry data from two females (17 total points), which likely biased the combined density estimates for this season. The best model was the trap-specific model (bk), with movement (σ) ranging from 0.88 to 1.05 km, the probability of detection (p) ranging from 0.01 to 0.03, and the density estimates (D) ranging from 34.5 to 41.78 individuals/100 km^2.

Habitat selection was estimated based on 434 telemetry locations from seven Geoffroy's cats (four males and three females). The top-ranked model included all three variables (native forest, distance to roads, and distance to water). Native forest and distance to roads positively influenced the habitat use of Geoffroy's cats, whereas the distance to water had a negative effect.

Our results indicated that Geoffroy's cats exhibit medium-to-high density in the Brazilian Pampa when compared to previously assessed populations of the species (Nowell and Jackson 1996; Cuellar et al. 2006; Pereira et al. 2011; Caruso et al. 2012; Tirelli et al. 2019). However, we observed that Geoffroy's cat population did not use habitats uniformly, selecting areas that were more distant from roads and closer to water and native forest (riparian forests). This preference for forested habitats may be related to increased resource (e.g., food and shelter) availability. Therefore, Geoffroy's cat preference for preserved areas while avoiding roads is likely to be a behavioral trait enabling this small cat to persist in a human-dominated landscape.

4.4.2 Margay's Persistence in Atlantic Forest Remnants

The margay (*Leopardus wiedii*) is a small wild cat distributed from northern Mexico to Uruguay and northern Argentina (de Oliveira et al. 2015). Margays seem to be strongly dependent on forested habitats (de Oliveira et al. 2015; Espinosa et al. 2018). This small cat is possibly the most arboreal of all felids (de Oliveira et al. 2015), presenting morphological adaptations that make them magnificent climbers. Their ankles rotate up to 180°, so they can hang upside down on trees, an ability aided by their long tail, which gives them balance (Macdonald and Loveridge 2010). Populations of small forest cats are understudied, mainly due to the difficulty in detecting them, particularly the specialized climbers, and to the logistic constraints of often working under very dense vegetation. As a result, solitary margay is the second least studied felid in South America (Macdonald and Loveridge 2010).

The Atlantic Forest is one of the areas presenting the highest habitat suitability for margays, so a large portion of the species distribution spreads along this domain, 92% of which is in Brazil. Although the margay is globally categorized as "Near Threatened" (de Oliveira et al. 2015), in Brazil the species is categorized as "Vulnerable" (Rio Grande do Sul 2014; Brasil 2022). Deforestation can negatively affect the populations of this forest-dependent species. In Horn et al. (2020), we estimated the population density of margays using SCR models across a range of areas with different levels of anthropogenic land-use changes and disturbances in the southernmost limit of the Atlantic Forest. We predicted that (i) densities would respond positively to forest cover, and (ii) densities would respond negatively to human disturbance and ocelot (*L. pardalis*) presence, as the presence of ocelots seems to negatively impact the densities of smaller, subordinate, felids, in a process known as "ocelot effect" (Oliveira et al. 2010).

Using 20 camera-trap stations per area (consisting of two digital cameras) in a 1-km grid, we sampled six areas, between 2017 and 2019, during summer and spring: TUSP (Turvo State Park), PROMATA (Pró-Mata Center for Research and Nature Conservation), SGNP (Serra Geral National Park), PFNF (Passo Fundo National Forest), TEUT (a rural area nearby the Teutônia municipality), and BPWR (Banhado dos Pachecos Wildlife Refuge). All areas were in the southern limit of the Atlantic Forest, with two of those areas (TEUT and BPWR) in the ecotone between the Atlantic Forest and the Uruguayan Savanna. Individuals were identified based on their unique spot patterns and sex was determined through the visualization of the presence/absence of male gonads. To investigate space use (σ), we used the individuals' sex as a covariate. To evaluate the detection rate (p) we used seven covariates related to competition (ocelots, domestic dogs, domestic cats), potential prey occurrence (small mammals, small birds), and the trigger speed and distance detection range of each camera trap. Finally, for fitting the density (D) models we used four spatial covariates: vegetation cover, distance to water, human population density, and distance to roads. In all parameters, we also evaluated the differences between the study areas, as these were located along a marked gradient of land-use intensity. Highly collinear covariates were excluded using the variance inflation factor >6 (VIF) (Naimi and Araújo 2016). We used multisession sex-structure SCR models to estimate σ, p, and D for the margay population in the study areas. We followed the workflow of the "oSCR" 0.42.0 package (Efford and Fewster 2013; Sutherland et al. 2019) in R (R core team 2020). We considered each sampled area as harboring a distinct margay population, due to the distance and the human-altered matrix between them. Therefore, each one represented an independent "session" in the analyses.

SCR analyses need a spatial extent, the state space (S). This is created by defining a buffer distance around the sites (camera-trap stations) and a specific resolution defining the state-space centroids, based on the session-specific trap coordinates. We used a buffer distance of half the movement (σ) estimated (2000 m) and a resolution value of half σ (Sutherland et al. 2019) (250 × 250 m). The nonhabitat points (e.g., water bodies) were clipped out from the buffers to avoid bias in the density estimates. We estimated density by using a three-step approach: (i) first we focused on the models for the parameter of the movement of the individuals (σ); (ii) in the second step we investigated potential effects of covariates in the probability of detection (p), including the best result of step one; and (iii) in this final step we allowed the D parameter to vary as a function of a single covariate or of an additive combination of two parameters ($D \sim$ [covariate], p [second step], σ [first step]). Models were ranked using the Akaike Information Criterion (AIC), considering equally fitted models with $\Delta\text{AIC} < 2$ (Burnham and Anderson 2002). The covariates presented in the top model or models were considered possible determinants of movement, probability of detection, and species density.

We recorded 66 independent margay records. Two areas were removed from the density analyses due to the low number of records (TUSP and SGNP). We were able to individually identify 23 margays in the remaining four areas. The top model included sex significantly influencing the movement parameter (σ), the number of independent records of small birds and mammals positively affecting the probability detection (p), and vegetation cover positively influencing margay's density (D). Density estimates varied between the areas: 9.6 ± 6.4 individuals/100 km^2 in BPWR; 37.4 ± 15.1 individuals/100 km^2 in PROMATA; 29.6 ± 11.4 individuals/100 km^2 in TEUT; 28.4 ± 12.5 individuals/100 km^2 in PFNF. Our results showed that males travel, on average, longer distances (1.19 km) than females (0.59 km).

Similar differences have been reported for this species in Mexico (Carvajal-Villarreal et al. 2012) and for other felids in the Atlantic Forest, including the jaguar and the ocelot (Goulart et al. 2009; Morato et al. 2016). More importantly, our data showed that margays occur at higher densities in areas with more vegetation cover, as initially predicted. This is certainly related to the arboreal habits of the species (Macdonald and Loveridge 2010; de Oliveira et al. 2015). The largest privately protected area of Rio Grande do Sul (PROMATA) was the area with the highest estimated density for the margay. This area is mostly occupied by primary forests and natural fields under natural regeneration from agricultural use for the last two decades (Blochtein et al. 2011), showing low levels of human disturbance (Graves et al. 2021). A potential good number of ancient trees, and subsequently arboreal shelters, and high prey availability are probably the reasons behind the high density of margays here. On the other hand, the lowest density estimate was obtained for BPWR. This area is located just 28 km away from Porto Alegre, the largest urban center in Rio Grande do Sul, where 1500 million people live (Graves et al. 2021). In BPWR, the landscape is dominated by open physiognomies, and, despite its protected status, the area suffers from land conversion for intensive agricultural schemes, water drainage, and illegal hunting. Noticeably, we expected to collect enough data to at least be able to estimate margay density in TUSP, the single best-preserved remnant of primary forest in Rio Grande do Sul, which was not the case; this probably relates to the high ocelot densities estimated for the area in the same period (see below), supporting our prediction that the presence of ocelots negatively impacts the densities of the smaller cats, the "ocelot effect" (Oliveira et al. 2010).

Overall, higher estimated margay densities were found in more preserved areas and the lower values in human-altered landscapes, supporting our hypothesis. In areas with moderate human land-use and reduced natural vegetation cover, we found intermediate values of density. This highlights the importance of preserving even the small native forest remnants in the highly fragmented Atlantic Forest.

4.4.3 Ocelots on the Edge

The ocelot is a solitary, medium-sized neotropical wild cat with a wide geographic range. The species is distributed from the southern United States to the northern part of Argentina and the southern part of Brazil (Paviolo et al. 2015). Because of this wide distribution, density estimates for the species range from 2 individuals/100 km^2 to 52 individuals/100 km^2 at SCR (Noss et al. 2012). Wildlife populations tend to have the highest densities in the center of their geographic range and lower densities at the borders of their range. The state of Rio Grande do Sul (Brazil) represents the meridional boundary of the global ocelot range (Paviolo et al. 2015). Here, little information is available on ocelot populations, and the species is categorized as Vulnerable (VU) (Rio Grande do Sul 2014).

Using the same sampling scheme reported above for the margay study, and by identifying each individual ocelot through its unique fur pattern, in Bolze et al.

(2021), we built five spatial capture–recapture (SCR) models in the package "oSCR" (Sutherland et al. 2019) from software R (R Core Team 2017): a null model, two with variations in the probability of detection (p), one with variation in individual movement patterns (σ), and a mixed model with variation in the two parameters (p) and (σ). To evaluate the models, we used the Akaike Information Criterion (AIC), and models with ΔAIC < 2 were considered equally well-adjusted (Burnham and Anderson 2002).

We found a total of 80 ocelot records in three of the six sampled areas, but only two areas had sufficient records to allow density estimation (TUSP = 72 and PROMATA = 7). The best-adjusted model for TUSP was the Mb (behavioral model), where the behavioral variable positively influenced the probability of detection $p(b) = 1.55$ ($p < 0.05$), showing trap-happy behavior by the ocelots. The estimated density for this area was 15.5 individuals/100 km^2 (±6 SE: Standard Error). In PROMATA, four density models were equally well-adjusted (ΔAIC < 2); among them, the null model M0 (ΔAIC $= 0$) predicted an average density of 27 individuals/100 km^2 (±24 SE).

Ocelots were only detected in the three least anthropogenically modified from the six sampled areas and, among those, most detections were in the single best-preserved remnant of primary forest in Rio Grande do Sul. This indicates that ocelot populations are negatively impacted by land-cover changes and, especially, highly dependent on well-preserved forests, as was previously shown by other colleagues (Massara et al. 2016; Cruz et al. 2018; Araújo et al. 2023). The low number of records in highly modified areas probably indicates the low densities of the species there, suggesting an ongoing process of local extinction, and the significance of well-preserved areas for top predator cats, like the ocelot.

4.4.4 Comparing Felid Densities in Rio Grande do Sul

Comparing the results of these three studies (Tirelli et al. 2019; Horn et al. 2020; Bolze et al. 2021), it is clear that native forests are critical to maintaining populations of these three cats in southern Brazil, although they are affected to varying degrees by land-use change and human disturbance (Fig. 4.5). Populations of ocelot are likely dependent on well-preserved fragments of seasonal deciduous forests in the Atlantic forest biome. Protected areas appear to be critical for the long-term maintenance of stable ocelot populations in the southern Atlantic Forest region (Bolze et al. 2021). Margay densities responded positively to vegetation cover, with higher density values in forested protected areas and intermediate density values in forested areas with some human modification. Unlike ocelots, this species can maintain populations in moderate human-altered forested areas and in transitional areas such as the ecotone between the Atlantic Forest and the Brazilian Pampa (Horn et al. 2020). The Geoffroy's cat appears to survive at relatively high population densities in human-dominated landscapes of the Pampa, whereas other predator species have already declined or disappeared altogether. This may be due to their

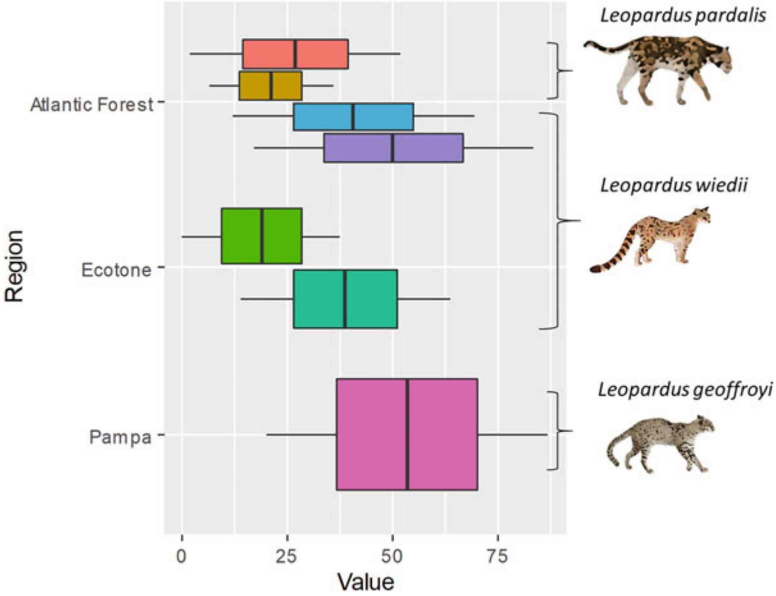


Fig. 4.5 Population density variations of ocelots (*Leopardus pardalis*), margay cats (*L. wiedii*), and Geoffroy's cats (*L. geoffroyi*) in Rio Grande do Sul state, Brazil. The plot was divided into three zones (Atlantic Forest biome, ecotone zone, and Pampa biome)

preference for riparian forests in these open landscapes. Most of the open habitats of the Pampa, such as the original grasslands, have been converted to cropland or cattle pastures, while the riparian forests are protected by law and no human economic activities take place in these areas. Therefore, we emphasize the importance of these areas in the human-dominated landscapes of the Uruguayan Savanna. Differences in tolerance to human-altered areas are evident for each of these cats, but in all cases, association with forested areas appears to be necessary for the survival of their populations.

4.5 Conclusion

This chapter provides an integrative review of previous research on the occupancy and density of neotropical mammals on the southern limit of the Atlantic Forest and the Brazilian Pampa. We emphasize the importance of using hierarchical modeling approaches to assess the effects of anthropogenic land-use changes on fossorial, flying, and terrestrial mammals. Our study found substantial variation in the occupancy and density of armadillos, bats, and carnivorans, with differential effects of human disturbance and landscape changes on their populations. In general, both terrestrial and flying mammals appear to prefer areas with higher levels of conservation, including small fragments of native vegetation, even when located in landscapes that have been heavily modified by humans and have low levels of connectivity. This underscores the importance of exploring the underlying mechanisms driving these effects, with particular emphasis on understanding the unique ecological requirements and conservation needs of individual mammal species. In addition, our results provide valuable insights into the ecology and conservation of neotropical mammals in human-dominated landscapes.

We suggest future research directions, including exploring the effectiveness of conservation strategies to mitigate the effects of human activities on mammal populations, assessing habitat connectivity, and examining the role of landscape structure in the conservation of neotropical mammals. Overall, our study highlights the need for continued research to support the conservation and management of neotropical mammals in the face of ongoing anthropogenic pressures.

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Chapter 5
Modeling the Abundance and Spatial Distribution of the Guanaco (*Lama guanicoe*) in Patagonia: A Review and Future Perspectives

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Abstract Understanding the factors that influence the abundance and spatial distribution of wild species has been of primary interest to researchers worldwide. This information has been generally considered to assess the status of populations and their habitat requirements and to make management recommendations related to

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their conservation and use. In South America, a species of particular interest is the guanaco (*Lama guanicoe*), given its adaptations and flexibility to occupy a wide variety of environments, its ecological role in the ecosystem, and its economic value in some regions. The guanaco has suffered a severe decline in numbers and a reduction in its geographic range since the 1800s due to legal and illegal hunting and the introduction of livestock (especially sheep). Currently, it occupies around 26% of its original range, and 81–86% of its global population remains in Argentina, with abundant numbers in Austral Patagonia. In this chapter, we review the different modeling tools that have been used to assess the status of guanaco populations throughout Patagonia, highlighting their advances, advantages, and limitations. We use study cases in different environmental conditions (e.g., spatial and temporal scales) to evaluate how local and regional contexts have impacted the abundance and spatial distribution of guanaco populations and to identify possible threats throughout their distributional range. Finally, we present some advances in innovative technologies that will improve detection during population surveys, which, in turn, will allow modeling with more accurate estimations.

Keywords *Lama guanicoe* · Spatial models · Patagonia · Population distribution · Habitat selection

5.1 Introduction

The guanaco (*Lama guanicoe*) is the artiodactyl that has occupied the largest geographic range in South America since the Pleistocene (Cabrera 1932; Menegaz et al. 1989: Fig. 5.1). Its distribution reaches different habitats from southern Peru to the southern limit of Tierra del Fuego (Cunazza et al. 1995; Wheeler 1995; Carmanchahi et al. 2019, 2022a). This species presents several physiological and anatomical attributes that allow it to adapt to diverse environments (Franklin 1983); these include three stomachs that facilitate the assimilation of nutrients; split lips that favor the trimming of vegetation; and molars adapted for the consumption of highly lignified vegetation (Franklin 1983). These adaptations allow the guanaco to make efficient use of the available trophic items and to have a highly variable diet.

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Fig. 5.1 A group of curious guanaco bachelors (*Lama guanicoe*) in La Payunia Reserve, Mendoza, Argentina. (Photograph by Antonella Panebianco)

The guanaco exhibits complex social behavior related to its mating system, forming social units that differ in size, territoriality, composition, and spatial distribution (Raedeke 1979; Franklin 1983; Panebianco et al. 2020, 2022). These social units are (1) family groups composed of a territorial adult male, several females and their offspring; (2) solitary territorial males that defend a small territory with females and young rarely present; (3) bachelor groups comprised of nonreproductive and nonterritorial males of all age classes (mainly juveniles); (4) female groups consisting of adult females, yearlings and offspring of both sexes; and (5) mixed groups consisting of males and females of all ages, and a highly variable group size that can reach hundreds of animals (Franklin 1983).

Although guanacos remain numerous and widely distributed, their populations have experienced a substantial decline since the nineteenth century due to excessive legal and illegal hunting, habitat degradation due to overgrazing by livestock, and interspecific competition (Baldi et al. 2010; Carmanchahi et al. 2022a). Its range has decreased by almost 75% of its original area of occupancy (Fig. 5.2; calculated by Ceballos and Ehrlich 2002, based on Franklin 1982). Currently, 81–86% of the individuals occur in Argentina, followed by Chile, which harbors around 14–18%. Both countries have the most abundant populations in the Patagonian region (González and Acebes 2016; Carmanchahi et al. 2022a). Although the guanaco appears as Least Concern in the IUCN Red List of Threatened Species (Baldi et al. 2016), such status does not consider the peculiarities of some populations, especially in the north of their range, where they are highly fragmented (Carmanchahi et al. 2022a).

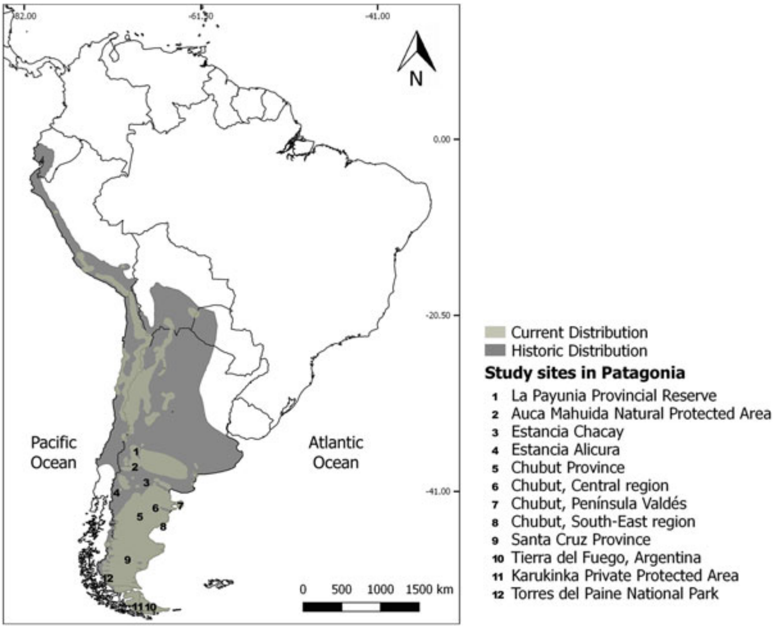

Fig. 5.2 Historic (dark gray) and current (light gray) geographic distribution range of the guanaco. (Modified from Carmanchahi et al. 2022a). Numbers in the map indicate the study sites in Argentinean and Chilean Patagonia, where modeling tools were implemented to study guanacos' abundance and distribution. 1 La Payunia Provincial Reserve (6650 km^2; Schroeder et al. 2013, 2014, 2018; Carmanchahi et al. 2014; Panebianco et al. 2022); 2 Auca Mahuida Natural Protected Area (770 km^2; Radovani et al. 2014; Rivas et al. 2015); 3 Estancia Chacay (400 km^2; Carmanchahi et al. 2014); 4 Estancia Alicura (150 km^2; Rey et al. 2009); 5 Chubut Province (2247 km^2; Pedrana et al. 2019); 6 Chubut, Central Region (170 km^2; Baldi et al. 2001); 7 Chubut, Península Valdés (4000 km^2; Burgi et al. 2012; Antún and Baldi 2020); 8 Chubut, South-East region (170 km^2; Baldi et al. 2001); 9 Santa Cruz Province (2459 km^2; Travaini et al. 2007, 2015; Pedrana et al. 2010); 10 Tierra del Fuego Province, Argentina (7107 km^2; Flores et al. 2018, 2020); 11 Karukinka Private Protected Area (3000 km^2; Moraga et al. 2015); 12 Torres del Paine National Park (1090 km^2; Iranzo et al. 2018)

Abundance and distribution estimates provide insight into aspects of population dynamics, that is, how a population copes with the challenges imposed by the environment and its variations over time; therefore, they are crucial components for the study of wildlife ecology. The abundance estimation presents a series of challenges related to the target species (such as behavioral traits), the environment, logistics, and budget (Iijima 2020). New models for abundance estimation are constantly developing and are a hot topic in animal ecology. For the guanaco, researchers have approached the abundance and distribution estimation through different methodologies, selected based on the objectives and constraints of each study.

In this chapter, we review the different modeling tools employed to assess the status of guanaco populations throughout Argentinean and Chilean Patagonia, highlighting their advances, advantages, and limitations. We use peer-reviewed study cases in various environmental conditions to evaluate how local and regional contexts have impacted the abundance and spatial distribution of these populations, identifying possible threats. Finally, we present some advances in innovative technologies that improve detection during population surveys, which, in turn, will allow modeling with more accurate estimations.

5.2 Modeling Guanaco Abundance and Distribution

In the last decades, interest in the spatial structure of the species has grown, resulting in new methodologies and more advanced models to predict the abundance and distribution of the species, and the factors affecting them. The studies about the spatial dynamics of guanaco abundance and distribution show these progressive advances in spatial modeling, highlighting how some methodological limitations have been overcome over time. In this section, we describe the methodologies and models applied to study the abundance and spatial structure of the guanaco throughout its wide distribution range in Patagonia.

5.2.1 Distance Sampling

Most density estimates of guanaco across Patagonia before the twenty-first century resulted from strip transects (Candia et al. 1993; Puig et al. 1997; Amaya et al. 2001). These estimates were achieved using a fully designed-based framework, which is beyond the scope of this chapter. However, it is worth mentioning that some key limitations of this technique include the assumption that all animals on the sampled plots are detected, ignoring the percentage of missing animals within the sampled area.

The first efforts to estimate the density and abundance of guanaco populations in Patagonia using modeling tools that incorporate detectability relied on distance sampling (Buckland et al. 1993). This technique involves recording distances from randomly placed lines or points to objects to model their detectability. Distance sampling is a hybrid technique since it involves a model-based approach to estimate a detection function that calculates the probability of detecting an animal within a certain distance of the line transect, and a designed-based inference to extrapolate density from the sampled plot to the survey region (Buckland et al. 2001; Thomas et al. 2010). In this way, objects can remain undetected in the surveys, which is one of the main advantages of distance sampling compared to strip transects (Buckland et al. 1993, 2001).

Conventional distance sampling (CDS) was first developed and refers to the case when the detection function is only modeled as a function of distance from the line (Buckland et al. 1993, 2001). Up to date, most studies that estimated guanaco density and abundance in Patagonia followed this methodology (Fig. 5.2; Baldi et al. 2001; Rey et al. 2009; Burgi et al. 2012; Carmanchahi et al. 2014; Radovani et al. 2014; Moraga et al. 2015; Travaini et al. 2015; Pedrana et al. 2019). Baldi et al. (2001) were the first authors that applied distance sampling to estimate guanaco abundance, accounting for its temporal and spatial variation in semiarid steppes of Argentinean Patagonia (Chubut province). The authors explored the relationships between guanaco and both sheep densities and the environmental availability of the most frequent plant species found in their diet's and tested predictions on the interspecific competition for food resources. Based on ground-based population surveys following the line-transect method at sites with different characteristics, they estimated the densities of guanaco and sheep using CDS and modeled guanaco density estimates using generalized linear models (GLM). Using this combined approach, the authors supported the predictions on the interspecific competition for limited food resources between guanacos and sheep (Baldi et al. 2001).

Many studies also used CDS to compare guanaco densities within and outside protected areas and assess changes in abundance after management actions (e.g., livestock removal) in many regions of Patagonia (Rey et al. 2009; Burgi et al. 2012; Carmanchahi et al. 2014). For example, Burgi et al. (2012) evaluated the response in guanaco densities after the creation of the San Pablo de Valdes reserve (Chubut Province, Argentina) and the removal of livestock in the area and then, compared these numbers with neighboring ranches with sheep presence over the same period. Following the line-transect method, they found that guanaco density increased three-fold within three years inside the reserve, while it remained relatively constant in the surrounding ranches, highlighting the effectiveness of management strategies and the value of modeling tools like distance sampling for assessing them.

Carmanchahi et al. (2014) also used distance sampling to evaluate the effects of guanacos' live shearing on density, group size, and spatial distribution in a partially migratory wild population inhabiting a protected area (La Payunia Provincial Reserve, Mendoza Province) and in a sedentary population living in a sheep ranch (Río Negro Province) in northern Patagonia, Argentina. Researchers found no significant differences in density and population structure before and after shearing activities in the sedentary population. In contrast, in the partially migratory population, animal density decreased, and the population structure changed significantly (i.e., a decrease in group size) after management activities. These parameters returned to premanagement levels one month later, concluding that the capture and handling of guanacos only had short-term effects on population parameters.

To date, there are fewer published studies on guanaco abundance and density using distance sampling in Chilean Patagonia. For example, Moraga et al. (2015) estimated guanaco abundance in Tierra del Fuego, the southernmost portion of its distribution range, to understand the effect of sheep ranching on guanaco habitat use. They recorded guanaco and sheep abundances by line-transect sampling along transects randomly chosen from all secondary roads and estimated density through CDS. Further analyses indicated that guanaco prefers open grasslands more than forests and zones where livestock densities are lower.

The first attempts to deal with heterogeneity in detections and improve the precision of the estimates using distance sampling were through stratification, which consists in dividing the data into subsets according to some covariate value and separately estimating the detection function for each of them (Buckland et al. 2001). Stratification is useful when (1) density or abundance estimates may be needed for individual strata, as well as for the entire study area; (2) density may vary considerably over the study region; or (3) different parts of the study region have distinct characteristics (i.e., variable detectability). The covariates include geographic region, environmental conditions, cluster size for clustered populations, habitat, and observer or platform. Stratification can be done before the survey when the information is available. Alternatively, poststratification can also be used based on data collected during the survey (e.g., social unit, habitat type, sex) producing separate density estimates, even though the design was not stratified (Marques et al. 2001).

In guanacos, Travaini et al. (2015) employed before and poststratification to estimate the variation in population size for Santa Cruz province (Argentina) derived from an extensive, large-scale road survey. Before conducting field studies, the authors divided the study area into 12 strata based on two environmental variables (Normalized Difference Vegetation Index – NDVI – and mean slope) to establish which tracks (road segments) would be surveyed. These two variables were selected since guanaco abundance might increase with vegetation productivity while detection might be affected by terrain irregularity. Environmental stratification before the survey helped reduce the variance of density estimates (Thomas et al. 2010). The authors then used this design to extrapolate density and distribution data beyond the sampled area and apply them to the whole range with similar environmental conditions (Travaini et al. 2007). Additionally, the authors classified guanaco groups into three observable social units with varying group sizes (i.e., breeding groups, nonbreeding groups, solitary individuals) during the surveys and used them as a form of poststratification to produce separate density estimates (Travaini et al. 2015).

Stratification in distance sampling does not always yield unbiased estimates. When animal density is low, small sample sizes may prevent subsetting the data and result in biased estimates of density (Marques and Buckland 2003). During the early 2000s, a new approach to address heterogeneity in detection probabilities was developed, making stratification less relevant (Marques and Buckland 2003; Buckland et al. 2004). This improved methodology allows the inclusion of covariates other than the distance from the line in the detection functions, that is, multiple-covariate distance sampling (MCDS; Buckland et al. 2004). MCDS may be advantageous when (1) we want to estimate the density for a stratum, but too few observations exist to fit a separate detection function; (2) the variance of the density estimates can be "explained" by variables other than distance; (3) density is correlated with detection probability. The covariates may relate to the individual detections (e.g., cluster size or animal behavior), the observer (e.g., observer ID) or the environment (e.g., habitat or weather), and can be either continuous covariates or qualitative factors (Buckland et al. 2004; Marques et al. 2007). As in any case of multiple-regression analysis, it is best to consider only covariates believed a priori to influence the detection probability (Marques et al. 2007).

MCDS has been applied to study guanaco populations inhabiting the southeast of Chilean Patagonia in Torres del Paine National Park. Because of protection policies, guanaco abundance in the park increased from less than 100 individuals to around 4200 in 35 years, expanding its distribution to surrounding areas from this National Park. Iranzo et al. (2018) detected this situation and assessed the spatial distribution patterns of guanacos' abundance, social structure and reproductive success using CDS and MCDS methods. The authors also compared the results within and outside Torres del Paine National Park to give a complete picture of the guanaco population and its colonization processes in the entire region. MCDS allowed adjusting the detection probability incorporating the guanaco group size as a covariate. The social structure of guanaco leads to the assumption that families, males, females, or mixed groups would be more detectable than, for instance, solitary males. Indeed, the models including group size as a covariate in the detection function were selected in winter when guanacos primarily gather in mixed groups, reaching up to hundreds of animals. The results showed that guanaco density was higher within the National Park than outside and that more than half of its population inhabits the neighboring ranches of the protected area, suggesting that guanacos have colonized these surrounding areas and are already well established. However, the authors suggested being cautious about these estimates owing to their high coefficient of variation. Such as they proposed, aggregated distribution patterns of animals could be the origin of those variations since it leads to large uncertainty in Distance software outcomes.

5.2.2 Species–Habitat Use Models Based on Presence/Absence Data

A major advance in the study of species distribution was the development and application of species–habitat use models. The main characteristic of these models is the ability to describe and predict the distribution of species in spatial and temporal maps at different scales, a principal application in conservation actions and management plans (Olea and Mateo-Tomás 2011). The species–habitat use models focus primarily on the location of occurrence data, Geographic Information Systems (GIS) summarizing the most relevant environmental gradients and landscape features of the study area, and statistical procedures. In this way, the species–habitat use models represent a suitable tool for analyzing the species–habitat relationship and showing these relationships through species occurrence probability maps (Gibson et al. 2004). In guanacos, species–habitat use models based on occurrence data were applied using three approaches: generalized additive models, resource selection functions and occupancy models. We discuss each of these separately.

5.2.2.1 Generalized Additive Models

The occurrence data used by species–habitat use models consist of presence–absence records where the most commonly used statistical procedures rely on generalized additive models (GAMs). GAMs are a flexible class of generalized linear models in which part of the linear predictor is specified in terms of a sum of smooth functions of covariates (Wood 2017). Travaini et al. (2007) described an integrated framework for modeling species distribution over vast areas that improved animal survey effectiveness by producing an effective way of gathering data, increasing the spatial accuracy of sightings, and decreasing error sources during data collection (see Fig. 5.2 in Travaini et al. 2007). The ultimate aim of this framework was to extrapolate species distributions from the surveyed region to a larger area based on the combination of remote sensing data, ecological modeling, and GIS. Following this framework, Pedrana et al. (2010) conducted ground surveys distributed among 12 strata and collected data on environmental and anthropogenic variables to analyze the relationship between guanaco occurrence and potential predictors in southern Argentinean Patagonia. This region has suffered from inadequate livestock management, including keeping sheep numbers above carrying capacity (Golluscio et al. 1998) and overgrazing of mesic sites (Mazzoni and Vázquez 2004). This species–habitat use model allowed the generation of predictive maps of guanaco spatial distribution at a regional scale. Based on a GAM, the authors found that guanaco occurrence increased in less productive and remote areas, far from cities and oil camps, and decreased in regions with high sheep density. These results suggest that human factors predominate over environmental variables in the guanaco distribution at the regional scale. Finally, using the model predictions, the authors built a probability map of guanaco occurrence, accounting for all the effects included in the model (see Fig. 5.2 in Pedrana et al. 2010).

In Chubut province (Argentina), where the human–guanaco relationship is also conflictive due to the presumed competition between guanaco and livestock for available forage and water (Carmanchahi et al. 2022b; Schroeder et al. 2022), Pedrana et al. (2019) applied species–habitat use models based on guanaco occurrence data and built predictive maps in a similar way to Pedrana et al. (2010). To assess which factors might influence the distribution of guanacos, the authors applied GAMs and selected potential predictors that summarized the most relevant environmental gradients and anthropogenic factors. Model results showed similar patterns to those found in Santa Cruz province – guanaco occurrence decreased with primary productivity and terrain elevation but increased with the distance to urban centers and oil camps (see Fig. 5.2 in Pedrana et al. 2019). The predictive map revealed a clear geographical pattern, with a gradient from low guanaco occurrence in the west (with higher productivity and more intense and sustained sheep ranching), to higher values in the east, where less productive and more arid areas predominate (see Fig. 3 in Pedrana et al. 2019). Altogether, the results found in both Chubut (Pedrana et al. 2019) and Santa Cruz (Pedrana et al. 2010) provinces suggest that guanaco distribution may not reflect a true habitat preference but an indirect response to exogenous factors – competition with sheep and a response to direct persecution by ranchers or poaching.

5.2.2.2 Resource Selection Functions

Resource selection functions (RSF, Manly et al. 2002) are other species–habitat use models widely used to describe, predict, and, ultimately, map the distribution of wildlife in terms of habitat suitability. Using statistical procedures often based on generalized linear models and their variants, the RSF estimates the (relative) probability of animal use of an area during a given time as a function of biotic and abiotic conditions that influence or account for selection. Different sampling designs of resource units can be used to detect resource use and selection that differ in the scope of inferences and applications: used/unused, used/available and counts of use designs (Manly et al. 2002). Schroeder et al. (2013) applied this analytical approach with a used/unused design to evaluate how interspecific interactions and environmental factors affect the resource use of guanacos and livestock in two seasonal periods in northern Patagonia. For such a design, the applied logistic regression provides estimates of the probability of use for a resource unit (i.e., Resource Selection Probability Functions, RSPF; Table 5.1). The authors found that guanacos used habitats with high temporal variability in plant productivity and away from potential human contact. Moreover, guanaco occurrence was inversely related to the presence of small livestock (goats and sheep) in spring-summer, but the reverse was not the case – guanaco presence did not explain the habitat use of large (cattle and horses) or small livestock in any season.

5.2.2.3 Occupancy Models

Occupancy models (OM; MacKenzie et al. 2002) are another modeling tool that has been used to analyze guanaco occurrence probability and its relationship with the factors describing the inhabited area (Rivas et al. 2015). OM relies on presence and absence data and incorporates the imperfect detection of organisms in the surveys by quantifying the detection probability. In this way, it is possible to determine the uncertainty associated with the detection in the sampled units (MacKenzie et al. 2002). There are different kinds of OM, depending on the analyzed number of species and the periods (single-species/two-species, single-season/two-season models). The type of OM depends on the study objective and hypotheses. The sampling design consists of a random selection of independent sampled units surveyed several times in one or more periods during which the occupancy (or lack of it) does not change. Using all the presence–absence records of each site, the detection and occupancy probabilities can be estimated. As a result, this occupancy probability can be related to the natural and anthropic factors affecting it and shown in habitat use maps.

Rivas et al. (2015) were the first researchers that applied OM to analyze the probability of guanaco presence in northern Patagonia (Argentina), where the predominant activities are small-scale livestock husbandry and the development of oil fields. The main goal of this study was to develop and test a sign-based

Table 5.1 A summary of the approaches and models applied to study guanacos' distribution and abundance in Patagonia

Approach	Model	Description	Model assumptions	Advantages	Disadvantages	Example
Distance sampling	Line-transect Distance Sampling	A suite of methods in which animal density and/or abundance is estimated from a sample of distances to detected individuals or indirect signs (e.g., pellet counts). The recorded distance of detected animals from the line is used to model a detection function.	1. Animals are distributed independently of the lines or points. 2. Objects on the line are detected with certainty. 3. Distance measurements are exact. 4. Objects are detected at their initial location.	Allows accurate estimates along line transect of individual and social group density and average cluster size using a simple and relatively low-cost methodology. Allows more accurate density estimates and their variances than traditional strip transects (Buckland et al. 1993, 2001).	A minimum number of observations (at least 60–80) is required to achieve a good estimation fit.	Baldi et al. (2001), Rey et al. (2009), Carmanchahi et al. (2014), Moraga et al. (2015), Travaini et al. (2015), Radovani et al. (2014), Iranzo et al. (2018)
Species–habitat use models based on presence/absence data	Generalized Additive Models (GAM)	Habitat models used for predictive occurrence and habitat modeling.	1. The probability of occurrence is homogenous inside the chosen grid cell size. 2. The spatial autocorrelation is negligible. 3. Absences are correctly estimated.	Evaluates covariables that affect the occurrence of a species. The user can include the proportion of the sampled area as a fixed variable in the model to compensate for the effect on the probability of detection (Travaini et al. 2007). It can describe and predict the species distribution in spatial and temporal maps at different scales. Allows the use of presence/absence data and count data.	Data are not corrected for imperfect detection. Do not take into account spatial autocorrelation.	Travaini et al. (2007), Pedrana et al. (2010), Pedrana et al. (2019)

(continued)

Table 5.1 (continued)

Approach	Model	Description	Model assumptions	Advantages	Disadvantages	Example
				GAMs are more capable of modeling complex ecological response shapes than GLMs (Yee and Mitchell 1991).		
	Resource Selection Probability Functions (RSPF)	Species–habitat use models based on used/unused design to describe predict and, ultimately, map the distribution of wildlife in terms of habitat suitability.	1. The probability of use is homogenous inside the chosen grid unit size. 2. Used locations are clumped due to habitat characteristics 3. Unused units (i.e., absences) are correctly identified	Evaluates the biotic and abiotic conditions that affect the probability of resource use in a given place and time (Lele and Kleim 2006; Johnson et al. 2006). It is possible to include the effective sampled area (i.e., the proportion of the units that had been surveyed, Travaini et al. 2007) as a fixed variable in the model to minimize the likelihood that units with 0 values were indeed units with undetected individuals.	Data are not corrected for imperfect detection, which limits the application and interpretation to the temporal and spatial domain of the sampling.	Schroeder et al. (2013)
	Single-season Occupancy model	Spatially explicit habitat models based on presence and absence data (obtained by direct counts or indirect signs from repeated	1. The species cannot be erroneously detected at an unoccupied sample unit. 2. Species detection at sample units is independent.	Evaluates the covariates that affect the occupancy probability and the extent of their effect (MacKenzie et al. 2002). Lower cost and more precise estimates (especially	The estimation of detection probability requires multiple sampling. The model's predictive capacity is limited to areas with similar	Rivas et al. (2015)

		observations) and the estimation of species' occupancy and detection capacity (MacKenzie et al. 2017).	3. The occupancy status at each sample unit does not change during the survey period. 4. The probability of occupancy is constant across all the sample units. 5. The probability of detection is constant across all the occupied sample units.	for species with low abundance) than other models based on abundance estimates (Rovero and Spitale 2016; MacKenzie et al. 2017). Occurrence data are relatively easy to collect; historical records can often translate into presence–absence data (Bailey et al. 2014). Provides means for estimating the detection probability and reduces bias through multiple sampling.	characteristics (natural and anthropic) to those of the surveyed units.	
Spatially explicit habitat models based on abundance data	Density Surface Modeling (DSM)	Spatially explicit habitat models of the abundance of a biological population corrected for uncertain detection via distance sampling methods and fitted by environmental heterogeneity (Miller et al. 2013).	1. Counts come from some count distribution (e.g., Poisson; negative binomial; Tweedie). 2. Counts and covariates vary between transects. 3. Variation of counts and covariates within units (i.e., segments) is minimal.	Evaluates the factors affecting population density/abundance/distribution by analyzing the interaction between covariates and count data. Allows the mapping of abundance values and their uncertainty in any subarea of interest. Allows extrapolation (with caution) of abundance estimates beyond the sampled area, which is	Did not allow using the year (i.e., the surveyed date) as a covariable in the model (but see Miller et al. 2021). The model's predictive capacity is limited to areas with similar characteristics (natural and anthropic) to those of the surveyed transects.	Schroeder et al. (2014), (2018), Flores et al. (2018, 2020), Antún and Baldi (2020), Panebianco et al. (2022)

(continued)

Table 5.1 (continued)

Approach	Model	Description	Model assumptions	Advantages	Disadvantages	Example
				often required by wildlife managers and decision-makers. Enables observations collected through “platforms of opportunity” (sampling that does not necessarily follow a pre-established design; Miller et al. 2021). Provides higher accuracy in abundance estimates compared to conventional design-based models by modeling their spatial variability (Buckland et al. 2001). Inference is less dependent on the region covered being a random sample of the study area but requires the model to extrapolate reliably.		

occupancy survey to help prioritize conservation interventions for large herbivores and identify how human activities might affect their conservation status. The authors applied a single-season single-species model based on walked line-transect sampling with spatial replication of surveys. Results showed that the sampling methodology evaluated is suitable and applicable in single-season occupancy models for guanacos, representing a simple and low-cost strategy to obtain a rapid assessment of guanaco distribution at a landscape scale. Guanacos were more likely found in higher and steeper areas and zones with fewer roads because poachers' access from towns, cities, and oil fields depends on available roads. Moreover, livestock density had the most negative effect on guanaco presence, suggesting that interventions reducing the impact of livestock would greatly affect guanaco's conservation.

5.2.3 Spatially Explicit Habitat Models Based on Abundance Data Corrected for Imperfect Detection: Density Surface Models

Following a model-based approach, density surface models (DSM; Miller et al. 2013) allow modeling spatial variation in density by combining distance-sampling theory with advances in statistical tools and geographic information systems. DSM opened new options for achieving unbiased and cost-effective estimates of species abundance and distribution at ecologically relevant scales. The latter has been a difficult task for large herbivores, such as the guanaco, which has extensive habitat requirements. DSM was first applied to terrestrial wildlife using the guanaco as a study model (Schroeder et al. 2014). Since then, this tool has contributed to expanding ecological and management knowledge of this species in different socio-ecological contexts of its South American range (Flores et al. 2018, 2020; Schroeder et al. 2018; Antún and Baldi 2020; Panebianco et al. 2022).

The main advantage of DSM is that it allows a reliable estimation of abundance and spatial distribution with its associated uncertainty in any area of interest within (and outside, but with caution) the study area. DSM improves the accuracy of abundance estimates compared to conventional design-based models built on distances since they model part of the spatial variability (Hedley and Buckland 2004). Using these models, Schroeder et al. (2014) predicted a maximum number of guanacos (25,951; CV = 0.16) for the northern area of La Payunia Reserve during spring, which was considerably higher than the total population size (10,000) estimated in the 1990s from direct animal counts using strip transects (Candia et al. 1993). The authors attributed the abundance differences to both counting methodology and population growth.

In general, many studies with a traditional design-based approach have stratified the surveys according to a unique variable assuming a species' homogenous distribution within each stratum. Such is the case for the guanaco in the Protected Area Peninsula Valdés (Northeast Patagonia), for which abundance estimations assumed

Fig. 5.3 Guanacos foraging in La Payunia Reserve (Mendoza, Argentina), which is characterized by vast flatlands in combination with areas with steeper hills and volcanic outcrops. (Photograph by Antonella Panebianco)

that the species showed a homogenous distribution within the vegetation physiognomic units (Baldi et al. 1997; Burgi et al. 2012). However, spatially explicit models showed that guanaco distribution and abundance are affected by several variables whose effects change in time and space. Antún and Baldi (2020) demonstrated that the guanaco is mainly affected by anthropic factors and heterogeneously distributed within each stratum of physiognomic vegetation units. Thus, the studies based on abundance estimations and guanaco distribution should consider the use of DSM since it might guarantee unbiased estimates without applying a random or stratified sampling design.

DSM modeling with data from different periods provided insight into the seasonal dynamics of guanaco abundance, leading to inferences about its migratory behavior, an increasingly rare event observed in terrestrial mammals worldwide. For example, in La Payunia Reserve (Fig. 5.3), guanacos showed a distinctive spatial and seasonal pattern of abundance, with a wide distribution and a maximum number of individuals in spring-summer. The opposite occurs in winter, when abundances can drop to less than 4000 animals, concentrated in a few medium-high density sites (Schroeder et al. 2014). Although the authors did not assess movement distances, their results indicate that most of the guanaco population moves outside the 1220 km^2 prediction area during the fall-winter period, suggesting a migratory behavior likely favored by the absence of physical constraints or other anthropic barriers in the area. In the Argentinean portion of Tierra del Fuego Island, the seasonal difference in abundance in the highest zones showed the guanaco performs altitudinal, migratory movements (Flores et al. 2018). The guanaco descends toward lower zones during the autumn-winter season, looking for food and a warmer temperature; during spring-summer, it returns to higher zones taking advantage of the available forage at an early ripening stage.

As discussed above, a relevant advance in model-based inference is the possibility of assessing the response of biological populations to biotic and abiotic factors that vary across study regions. In this sense, responses measured as abundance rather than binary presence/absence data not only allow the development of more biologically informative models but also overcome the problem of correctly estimating absences. In the case of guanacos, factors related to anthropic pressure as well as environmental conditions have proven to be good predictors of guanaco abundance in different scenarios and scales of their Patagonian range (Schroeder et al. 2014, 2018; Flores et al. 2018, 2020; Antún and Baldi 2020; Panebianco et al. 2022). For example, Antún and Baldi (2020) proved that abundance patterns in terms of food preferences and predation risk were opposed in scenarios with contrasting anthropic levels in Península Valdés (Chubut province, Argentina). In the Argentinean portion of Tierra del Fuego, another study showed that this species responds to forage availability (Flores et al. 2020), occupying areas with intermediate quality and quantity of food in the reproductive season but higher availability in the nonreproductive season. At a Patagonian site with limited poaching, Schroeder et al. (2018) found no relationship between guanaco abundance and proximity to roads at either the site or patch scale during any season, regardless of the traffic disturbance associated with roads. Finally, Panebianco et al. (2022) applied DSM to assess the influence of bottom-up, top-down, and social factors on the spatial distribution of territorial male guanacos in a semiarid ecosystem during the reproductive season. The authors found that in these low-productivity environments, bottom-up (primary productivity) and social traits (female grouping) predominate in regulating the spatial distribution of territorial male guanacos rather than top-down factors (correlates of predation risk).

As illustrated in the previous sections, a long-standing concern in the study of the guanaco has been its interaction with domestic herbivores, not only from an ecological but also from a management point of view. Many studies used DSM to explore habitat use and niche partitioning between herbivores as a means of inferring competition. For example, Schroeder et al. (2014) combined density surface and null models of abundance data to analyze the spatial and seasonal dynamics of abundance and distribution of guanacos and domestic herbivores in northern Patagonia. By visual comparison of abundance maps and co-occurrence analyses, the authors demonstrated that herbivores were not randomly distributed across the landscape, that is, the abundance of guanacos and small livestock negatively covaried in all surveys more than expected by chance. These results suggest a competition mechanism between ecologically similar herbivores, although various environmental factors could also contribute to habitat segregation. Flores et al. (2020) also detected a negative relationship between guanaco and livestock abundance using DSM, but in this case, for guanaco family groups. The groups with a larger ratio of younglings to adults occupied territories with less livestock abundance but an intermediate quantity and quality of forage. Similarly, Antún and Baldi (2020) applied DSM to study the interactions between guanacos and livestock in two contrasting contexts in northeastern Patagonia – in areas with sheep ranching and where the activity has ceased but fences and other infrastructures remain in place. In the absence of livestock, the authors proved that the spatial structure of guanacos shows habitat preferences for open areas with a predominance of grasses and herb species (Puig et al. 2008; Burgi et al. 2012; Moraga et al. 2015). They also demonstrated that human-related effects, such as infrastructure, are still significant and negatively affect guanaco's abundance.

5.3 Methodological Aspects of the Modeling Tools Used on Guanacos

Large-scale modeling of species distributions and abundances must deal with several methodological issues related to data collection, experimental design, and statistical procedures. Many of these are inherent to each tool, including imperfect species detectability, the low spatial accuracy of records, and unknown contemplation of the sources of variation affecting animal sightings. Furthermore, it is worth mentioning that gathering field observations over large areas is expensive, time-consuming, and susceptible to mistakes. In this section, we discuss some key aspects of the modeling tools reviewed in the previous section, highlighting the advantages and disadvantages in each case (Table 5.1).

5.3.1 Distance Sampling

The most relevant design and model assumptions in distance sampling are described in Table 5.1. As in most modeling tools, designing the survey and field methods considering the key assumptions is more satisfactory than attempting to solve problems arising from assumption failure at the analysis stage (Buckland et al. 2015). A suitably randomized design will ensure that the design assumption (i.e., animals are distributed independently of the lines) holds, for example, by randomly placing a systematic grid of lines throughout the study region. In terrestrial surveys, this is often difficult to achieve; researchers end up using roads or tracks as line transects (Baldi et al. 2001; Rey et al. 2009; Burgi et al. 2012; Carmanchahi et al. 2014; Iranzo et al. 2018). Densities along roads and tracks may not be representative for many reasons, such as increasing disturbance, avoiding less accessible terrain and habitats, or creating open space and edge habitats that may attract animals (Buckland et al. 2015). In turn, it may present problems when inferring the abundance of the total study area (Buckland et al. 2001).

To compensate for potential biases related to nonrandom sampling, studies in guanacos used some form of randomization, in which observers traveled to randomly selected positions and set transect origins and directions within a feasible radius (Moraga et al. 2015). For example, Travaini et al. (2015) randomly selected road segments of available tracks, defined as complete or fractions of stretches between crossroads. Furthermore, the authors argued why the distribution of guanacos was independent of roads and preliminarily concluded that biases in the density estimates due to violating this assumption were implausible.

Two alternative survey methods could serve to follow a random sampling design, although both present challenges. Terrestrial line transects on foot or horseback could be difficult to perform far away from human settlements (with the consequent bias), making it difficult to cover large regions over a short period and may be more expensive than vehicle-based surveys. In addition, these alternatives may not be more adequate than road transects because the observer would move too slowly in relation to guanaco movements, adding a new source of bias from the nonresponsive movement of animals. Aerial surveys from a plane could solve some of these problems but are more expensive than terrestrial surveys and present many logistic issues (e.g., the design must consider proximity to airports). New technology, such as unoccupied aerial systems, is emerging as a novel surveying methodology that could ensure random sampling design and solve several drawbacks that affect the other alternatives mentioned above (see the next section on new technology).

Random transect placement is always recommended. Only when it is not possible, researchers should consider placing transects along with landscape features, tracks or roads and state it when reporting results, discussing the potential implications given the characteristics of the target species (Marques et al. 2010; Travaini et al. 2015). Another option is to conduct a pilot study to assess whether roads generate a type of avoidance or attraction behavior in the species of interest, as shown by Schroeder et al. (2018). Moreover, we recommend following Buckland et al. (2015) who suggest a set of methods to correct for bias in nonrandom transect placement, including additional data collection that could help obtain more robust estimates.

5.3.2 *Species–Habitat Use Models Based on Presence/Absence Data*

As seen earlier, many statistical tools are available to model presence–absence data. These models share some assumptions and many advantages (Table 5.1). For example, they all require defining homogeneous sampling units. Unit size depends on the ecology of the target species (e.g., distance traveled per day, home range), the sampling method used (e.g., camera-trap site, transect segment), the study objective (e.g., species–habitat preferences, priority areas for conservation), and the spatial and the temporal scale in which the natural and anthropic variables vary. Sometimes, sampling units are defined by the spatial resolution of the predictor variables, especially when using remote sensing data (Travaini et al. 2007; Pedrana et al. 2010, 2019; Schroeder et al. 2013).

Choosing the adequate sampling units has implications for spatial autocorrelation, which arises when environmental processes and patterns that influence the spatial distribution of wildlife are spatially structured and/or the species is subject to demographic processes, animal behavior or dispersal limitations (Wintle et al. 2005). Autocorrelated observations are not independent and can interfere with statistical inference, leading to an underestimate of standard errors or an overestimation of the importance of habitat variables (Legendre and Fortin 1989). Many tools exist to assess the extent of spatial autocorrelation in model residuals, the most commonly used being correlograms and variograms. Other approaches include modeling animal contacts at a spatial resolution that sightings may be independent (Boyce 2006) or using goodness of fit assessments (MacKenzie et al. 2017).

GAM and RSPF also assume that unused units (i.e., absences) are correctly identified (Table 5.1). Occasionally, this is difficult to demonstrate, especially for mobile and cryptic animals (Boyce et al. 2002). Additionally, at times, the unused site classification depends on the intensity of the sampling. However, calculating the effective sampled area and including it as a fixed term in the models could compensate for its effect on the probability of detection (Travaini et al. 2007; Pedrana et al. 2010, 2019; Schroeder et al. 2013).

Occupancy models stand out from other models by estimating the uncertainty in the detection, making it possible to determine the actual occupancy and the species detection probabilities in the sampled unit or site. OM has some specific assumptions that are important to highlight (Table 5.1). First, it is assumed that there are no false positives (erroneously detecting individuals at an unoccupied sample unit), which could lead to biases associated with the occupancy estimators (McClintock et al. 2010; Miller et al. 2011). This error usually depends on the difficulty of identifying the study species, the experience of the observers, the survey area, and the survey design. Fortunately, statistical tools of OM sometimes allow for handling false positives and guaranteeing unbiased estimations by redefining the false detection in probabilistic terms related to the occupancy and observation processes (assuming a false detection probability at unoccupied sites). However, this process implies more complex models (a greater number of parameters), and the capacity to obtain reliable estimates will depend on the amount and variety of data (number of records; the percentage of data without false positives; Clement 2016). Second, if occupancy and detection probabilities are heterogeneous, they should be modeled by covariates at the site and observational level. In these cases, the model must have not correlated covariates that could explain the before-said heterogeneity. For this requirement, the survey design must consider the target species' ecology and the variables that vary across the survey area.

5.3.3 Spatially Explicit Habitat Models Based on Abundance Data Corrected for Imperfect Detection: Density Surface Models

As we described above, DSM estimates the density/abundance of biological populations through spatially explicit modeling of the detection-corrected count data. Data come from line or point transects; if using lines, they are divided into contiguous segments (Miller et al. 2013). Modeling consists of a two-stage approach that involves (1) fitting a detection function to the distance data to obtain detection probabilities of individuals/clusters and (2) building a GAM (Wood 2017) with either summarized counts or estimated abundance by distance sampling per segment/point as the response variables. The area of segments is frequently set to a square surface according to the truncation distance (w), such as $2w \times 2w$. Each segment summarizes the environmental covariates modeled through smooth functions as splines, providing flexible unidimensional (and higher-dimensional) curves (and surfaces, etc.) that describe the relationship between the covariates and response (Miller et al. 2013).

Although the correction by imperfect detectability is one of the most relevant DSM advantages (Table 5.1), it is also possible not to consider it. This implies assuming a uniform detection function for the count data in the first stage. For example, Flores et al. (2018, 2020) used aerial surveys to record the guanaco abundance in Tierra del Fuego (Argentina), unable to register the cluster/individuals' distance from the flight path. Aerial surveys allowed the authors to sample independently of the roads' influence, reach inaccessible zones, cover a large area within a short time, and, most importantly, capture the environmental heterogeneity in the area of interest. As DSM is a model-based inference approach, the data range should include the environmental variability of the nonsurveyed sites (Miller et al. 2013). Considering the advantages of aerial surveys to supply this sampling requirement, Flores et al. (2018, 2020) recorded the data following the strip-transect method. Furthermore, a pilot test showed that none of the most frequently used detection function models performed better (Uniform, Uniform + cosine, Hemi Normal + Simple polynomial and Hazard + Hermite polynomial), allowing the researchers to apply DSM without accounting for imperfect detectability.

DSM allows an understanding of how abundance varies in relation to environmental heterogeneity. That is the percentage of deviance explained, which values are frequently low for large herbivores (Valente et al. 2016) probably because the selected spatial scale to build the models does not match those that the animals use to make decisions. For guanacos in Tierra del Fuego, for example, it was suggested to perform the analysis with a smaller scale rather than 1.96 km^2 (Flores et al. 2020) since the feeding area approximated to 0.3 km^2 and the mating territory to 0.25 km^2 (Puig and Videla 1995; Young and Franklin 2004). Two issues could hamper the correct selection of the spatial scale: (1) decreasing or increasing the area of the segments could prove difficult because it relies on the truncation distance or the effective area for segments, and (2) covariates variation in the segments could be high to capture the animals' response to environmental heterogeneity. It is advisable to check if the covariates' variation in the landscape allows us to build homogeneous segments before running the analysis and if those segments correspond with the animal's environmental selection scales.

In spatially explicit models, spatial autocorrelation is considered inherent to the landscapes, and one of the structural attributes that one seeks to understand when applying this type of habitat models (Boyce 2006). In the case of DSM, using smooth of locations is often a simple way to account for spatial autocorrelation between segments (within transects), and as a proxy for other spatially varying covariates that are not available (Miller et al. 2013; Schroeder et al. 2014; Antún and Baldi 2020; Panebianco et al. 2022). Another more complex way to account for spatial autocorrelation is to explicitly introduce correlations into the DSM using tools such as generalized additive mixed models (GAMM; Wood 2017) to build an autoregressive correlation structure (Miller et al. 2013).

5.4 New Technology and Future Perspectives

Over the last decades, we have experienced tremendous technological advances that have led to new opportunities in wildlife research, improving aspects of data collection and developing new and improved statistical tools and software analysis, among others. Here, we highlight some recent advances, with a focus on the study of large mammals, like guanacos.

5.4.1 Using Technology to Collect Data

Building large data sets and reliably transforming them into analyzable data sheets requires continuous innovation in data-collection methods (Wich and Piel 2021). Traditional techniques depend on paper sheets or tape recorders to register wildlife sightings (Fuller and Mosher 1987). Although highly flexible, record sheets are bulky and require stopping the vehicle to fill out the forms. A tape recorder might be more convenient because the information can be dictated without stopping the vehicle but is more prone to errors because there is no visual confirmation that all the appropriate data has been recorded correctly. These methods also require significant time to transcribe the data and may introduce a new source of error. For guanacos, some studies have benefited from the registration of sightings during fieldwork using digital forms and free software (such as Cybertracker) incorporated into a Personal Digital Assistant (Travaini et al. 2007, 2015; Pedrana et al. 2010, 2019). Today, the massive use of smartphones has become a powerful and increasingly accessible tool, with multiple features (e.g., GPS, camera, Bluetooth) that scientists could explore to improve the quality of data collection (see Wich and Piel 2021).

5.4.2 Advances in Surveying Methods

Ecological research and effective wildlife management rely on the accurate and precise monitoring of the number and distribution of animals, which can pose logistical and analytical challenges for large-bodied wild species because of their extensive habitat requirements. Piloted aircraft sampling gained popularity and relative confidence as a traditional method but remains cost-prohibitive in many locations and contexts. Ensuring unbiased and cost-effective estimates have led ecologists and wildlife managers to continue developing more accurate methodologies.

In recent years, Unoccupied Aerial Systems (UAS, also called drones) have emerged as an attractive new tool and given their comparative advantages, are rapidly replacing conventional sampling methods. Drones are safe for operators, relatively less noisy than piloted aircrafts and able to access dangerous or remote areas. They allow for repeating the same flight plan over time, capturing images with user-defined resolutions, and carrying more than one sensor (e.g., a thermal camera, Chrétien et al. 2016), considerably improving the quality of the data obtained (Hodgson et al. 2018). Moreover, images provide a permanent recording of data that can be revisited and analyzed again in the future for unforeseen research questions. Research on drones' use in wildlife is still in the trial phase; each environment and target species represents a particular challenge. For example, in arid open environments such as those inhabited by guanacos, with relatively good visibility to detect animals but little environmental noise, there is a trade-off between flying the UAS high enough to diminish the disturbance due to the noise level of the drone engine, while maintaining count precision in the images. Based on three types of experimental flights, Schroeder et al. (2020) demonstrated that the likelihood of miscounting guanacos in images increases with UAS height, but only for offspring, as expected due to their smaller size compared to adults. The authors suggest that further training of the observers, together with the use of digital postprocessing tools, would help not only reduce potential errors in offspring counting but also overcome the limitations of the considerable effort required to process the images. There are promising recent examples of the use of special software to assist manual counting of animals in images (Ersts 2019), as well as semiautomatic and automatic identification systems and counting algorithms (Lhoest et al. 2015; Gonzalez et al. 2016; Rush et al. 2018). In addition, UAS image-based counting of individuals has shown improved accuracy compared to ground-based counts (Hodgson et al. 2018; Rush et al. 2018; Bröker et al. 2019).

When using drones for wildlife monitoring, the disturbance to target species must be kept to a minimum to reduce behavioral responses that could lead to detection bias. Unfortunately, this is an underexplored and increasingly urgent issue. Up to date, only a few planned and systematic studies assessed the potential effects of drones on wildlife, and only recently has it been acknowledged as relevant to prevent and mitigate drone-associated disturbances. To fill this information gap, Schroeder and Panebianco (2021) used the guanaco as a study model to experimentally address this issue. Taking advantage of the complex social behavior of this species, they investigated how sociability, together with flight plan characteristics, influences the behavioral responses to drone-associated disturbances, as it has been proposed that living in groups may be a strategy that enhances the effectiveness of prey animal responses to perceived threat stimuli (Frid and Dill 2002). The authors found that large groups were more reactive and less tolerant (i.e., greater flight distances) than small groups and solitary individuals, regardless of the presence of offspring. These results suggest that sociability allows guanacos to improve their capacity to react to human-associated disturbances, like drones, probably due to increased detection ability in larger groups. As expected, low flight heights increased the probability of reaction, although the effect of drone speed was less clear. Finally, based on the information on flight distances, the authors estimated reaction thresholds and flight heights that could minimize disturbance. Moreover, to reduce reaction distances of sensitive species, the authors recommend (1) prioritizing small multirotor drones; (2) using low-noise propellers; (3) when possible, conducting surveys when large groups are less common in the population (e.g., during mating season); and (4) assessing whether animals habituate to repeated drone exposure, as found in other taxa (Brisson-Curadeau et al. 2017; Rümmler et al. 2018; Ditmer et al. 2019).

The combination of new data-capture technologies, such as drones and machine learning, combined with abundance-modeling tools that account for imperfect detection shows a promising future field of research and application in wildlife monitoring. Although in its infancy, some recent examples show enormous potential. First, the transition from a method of data collection through direct human observations to one using unoccupied aerial imagery involves rethinking the conventional methodology in terms of sensor detection capabilities and flight autonomies, regulatory constraints on UAS use, and the mobility of animals along with the associated spatial scale. For example, Cleguer et al. (2021) developed a small UAS-adapted wildlife survey method based on a grid sampling design using two multirotor drones (Phantom 4 Pro) flying simultaneously within the permitted field of view and from a vessel base station. They used this protocol in combination with DSM to estimate the fine-scale distribution and abundance of dugongs (*Dugong dugon*) in Western Australia. The authors concluded that their method was convincing in a real-world application because of its feasibility, ease of implementation and achievable area coverage. In turn, it has the potential to be used in a wide range of applications, from local-scale community-based surveys to long-term repeated surveys. Going a step further, Brack et al. (2023) assessed the performance and optimal sampling design (i.e., number of visits and number of sites) of hierarchical N-mixture models, focusing on drone-based surveys. N-mixture models provide a useful tool for studying unmarked populations since they allow modeling the abundance from multiple surveys while accounting for imperfect detection (Brack et al. 2018). The authors simulated count data considering different scenarios of local abundance and detectability of individuals and compared single-observer versus double-observer protocols (human observer or machine learning algorithm) in image review. Their results showed that the accuracy of abundance estimation with N-mixture models depends on the availability of individuals to be detected and can improve with double-observer protocols. Altogether, this study demonstrated that drone-based surveys combined with hierarchical models are powerful tools that can be adequate to estimate abundance in a variety of contexts, including studies in which the availability of individuals and/or population density are low (e.g., forested areas and threatened species).

5.4.3 Overcoming the Challenges of Combining Data from Multiple Platforms

Studies involving wildlife monitoring typically require extended datasets. As a recent technique, having a large amount of high-quality data from UAS imagery presents the challenge of integrating it with previous data from conventional survey methods. Combining data from multiple platforms is particularly useful for long-term studies but also when working with cryptic species for which data is difficult to obtain or endangered species that require management decisions. A recently developed analytical strategy consists of modeling the different data observation processes from multiple platforms as separate detection functions and then integrating these functions into a single spatial model that accounts for varying detectability conditions (Miller et al. 2021). Platforms can be physically different surveys conducted via several means (e.g., aerial and terrestrial, or surveys taking place at different times), different protocols taking place in the same survey (e.g., birds on the water via line transect and those flying via strip transect), or some combination of these (Miller et al. 2021). When conducting a video/photo survey from an aircraft or drones, strip transects are commonly used, which assume that object detection is certain. In these cases, the probability of detection is equal to 1 (i.e., the detection function is uniform, but see Brack et al. 2018). By applying this approach to two marine species, the authors state that this methodology enables more robust abundance estimation, potentially over wider geographical or temporal domains (Miller et al. 2021).

5.5 Final Considerations and Conclusions

In this chapter, we review the variety of approaches and modeling tools that many researchers have applied to study the distribution and abundance of guanacos in Patagonia during the last two decades. These studies illustrate the advance in the development and complexity of models over the years, which have allowed us to understand the relationship of this species with its environment, evaluate ecological processes such as interspecific competition or density-dependence, and assess the impact of the management activities on this species. However, the most complex and sophisticated tools are not always the best option – the choice of the optimal approach will depend on the objectives of the study, the ability to meet the assumptions, the spatial and temporal scales, the characteristics of the target species, and the possibility of solving logistical issues, among other factors.

Based on the review of studies that assessed guanaco distribution and abundance in Patagonia, we can identify some information gaps and potential threats throughout its range. First, we found only a few papers that studied the density and abundance in Chilean Patagonia, which was previously reported by Moraga and Vargas (2018). We believe the information provided in this chapter could represent a valuable basis for learning about successful case studies and the variety of tools available. Second, a common factor in most of the papers reviewed was the interaction between guanacos and livestock. As we highlighted in the previous sections, this species has historically been perceived as a threat to livestock husbandry, as it shares the diet and habitat with domestic herbivores (Schroeder et al. 2022).

In southern Argentinean Patagonia, there is a widespread perception that guanaco populations have recently increased in numbers, to the extent that Santa Cruz province attempted to declare it a pest species in 2012, authorized actions to reduce guanacos' numbers within ranches, and promoted changes in national public policies related to guanaco management (Carmanchahi et al. 2022b; Lichtenstein et al. 2022). These actions were promoted without having updated and reliable abundance estimates for this species (Fig. 5.4). In this sense, knowing "how many guanacos there are and where they are" is a continuous source of dispute among the different sectors

Fig. 5.4 Hillsides give guanacos a privileged view. (Photograph by Antonella Panebianco)

interested in the management of this species. Finally, different modeling tools were used to assess the success of conservation and management actions in many Patagonian sites, which can complicate comparisons and estimation of regional trends. Having a reliable and validated sampling and analysis method, technically and logistically possible, that allows knowing the distribution and abundance trends of the guanaco at both the local and regional scales is still a challenge to overcome. Although some efforts have been made to standardize survey methodologies and data analysis for management purposes (Baldi et al. 2006; SAyDS 2019), we must continue to develop and refine planning tools, including habitat modeling methods, with an emphasis on statistical and ecological rigor and simplicity (Wintle et al. 2005).

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Chapter 6
Survey Methods and Hierarchical Modeling for Mexican Primates

Anja Hutschenreiter, Carmen Galán-Acedo, Denise Spaan, and Filippo Aureli

Abstract The Southeastern part of Mexico is inhabited by two species of howler monkeys (*Alouatta palliata, Alouatta pigra*) and one species of spider monkey (*Ateles geoffroyi*), thereby making Mexico the most northern distribution of Neotropical primates. All species are Endangered according to the IUCN red list; thus, accurate abundance estimates and evaluation of population threats and trends are indispensable to establish effective conservation measures. Hierarchical models are a powerful tool for gathering such information and obtaining comparable results across surveys and study sites. We conducted a literature review to evaluate the eligibility of hierarchical modeling for studies involving data from surveys of Mexican primates. We found recce walks to be the most commonly used survey method for Mexican primates, and both abundance and presence/absence-related outcomes to be the most frequently reported response variables derived from such surveys. The vast majority of studies did not take heterogeneity in detection probability into account, potentially causing bias in results, and often did not use inferential statistics for hypothesis testing. Whereas only one study has used

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hierarchical modeling for Mexican primate abundance estimates so far, we show that hierarchical models are very suitable for data gathered using both traditional and recently developed survey methods for spider and howler monkeys. We particularly advocate for an increased application of hierarchical models using presence/absence data for species with a high degree of fission–fusion dynamics, which impedes reliable counts at the individual and group levels.

Keywords Detectability · Drones · Fission–fusion dynamics · Monitoring · Occurrence · Passive acoustic monitoring · Sampling

6.1 Introduction

Hierarchical models have gained popularity in the field of mammal population ecology over the last two decades for various reasons. Hierarchical models estimate animal occupancy (i.e., the probability of an animal being present within an area) or abundance (i.e., the number of individuals or groups within an area) based on data from repeated surveys, and only a few assumptions are required to be met for their use (Royle and Dorazio 2006). Similar to distance-sampling approaches (Buckland et al. 2015), hierarchical modeling approaches assume the sighting of an animal to be influenced not only by the actual number of individuals present in the survey area but also by the probability of detecting the animal (Bolker et al. 2008; Royle and Dorazio 2006). Whereas the variation in animal abundance and occupancy depends on habitat characteristics and other climatic and ecological factors that influence the distribution of a species at large and small spatial scales, the variation in detection probability depends on factors that enhance or reduce the observer's ability to detect an animal (Dénes et al. 2015). The latter factors include weather conditions during a survey, vegetation density at a site, and survey effort. Hierarchical modeling allows for more accurate and unbiased estimation of different aspects of species ecology by including covariates expected to affect detection probability independently from covariates affecting the species' presence or abundance at a site (Royle 2004). In contrast to multiple-covariate distance-sampling approaches (MCDS, Marques et al. 2007), detection probability in hierarchical models can be estimated independently from the perpendicular distance between the observer and the animal sighted and include any other potentially relevant factor. This feature makes hierarchical modeling an ideal and flexible tool to be applied to data from surveys in which animals on the transect center-line are not detected with certainty and to be combined with a whole range of survey methods that do not allow for distance estimation, including the combination of multiple survey methods.

Although mostly applied to data from camera-trap surveys (Rovero and Spitale 2016), hierarchical modeling can easily be applied to data collected using more recently developed survey methods such as aerial or acoustic monitoring (Kalan et al. 2015; Williams et al. 2017). Besides its independence from animal–observer

Fig. 6.1 The three Mexican primate species: (**a**) Geoffroy's spider monkey, (**b**) the black howler monkey, and (**c**) the mantled howler monkey. (Photo credit: Fabrizio Dell'Anna, Denise Spaan, and Ben Keen [licensed under creative commons share alike [CC BY 4.0, https://www.inaturalist.org/photos/164443433?size=original])

distances, the use of hierarchical modeling requires fewer sightings than distance sampling, which makes it applicable to surveying species that occur at low densities. Whereas 60–80 sightings are required to apply distance sampling to data from line-transect surveys, and 75–100 sightings to data from point-transect surveys (Buckland et al. 2001), complex hierarchical models can be run with fewer sightings depending on the detection probability and true occupancy or abundance of the species of interest (Guillera-Arroita et al. 2010; Guillera-Arroita and Lahoz-Monfort 2012). For instance, 42 detections of Geoffroy's spider monkeys (*Ateles geoffroyi*) were sufficient to fit Royle–Nichols models with eight site-level covariates in a recent study (Hutschenreiter et al. 2022). Despite its flexibility, hierarchical models have not yet received much attention in research on Neotropical mammals that are not commonly monitored with camera traps such as primate species.

Mexico is the northernmost distribution of Neotropical primate species. Only three species from two genera inhabit the country: the Geoffroy's spider monkey (*Ateles geoffroyi*), the black howler monkey (*Alouatta pigra*), and the mantled howler monkey (*A. paliatta,* Fig. 6.1). Whereas Geoffroy's spider monkeys are widely distributed from central to eastern Mexico, including most of the Yucatan Peninsula, the distribution is limited to central Mexico for the mantled howler monkey and mainly to the Yucatan Peninsula and part of central Mexico for the black howler monkey (Calixto-Pérez et al. 2018). All three Mexican primate species perform important ecological roles as seed dispersers (Fuzessy et al. 2017; González-Di Pierro et al. 2021) and face declining populations due to habitat loss, habitat modification, and hunting (Arroyo-Rodríguez and Dias 2010; Oropeza Hernández and Rendón Hernández 2012; Méndez-Carvajal et al. 2022). As a result, all Mexican primate species are Endangered according to the IUCN red list (Cortés-Ortíz et al. 2020; Cortés-Ortíz et al. 2021; Cuáron et al. 2020). Therefore, large-scale population monitoring is crucial to accurately document population trends and determine important predictors of species' occurrence and abundance, providing vital information to develop targeted conservation management plans. Effective survey methods and flexible options for data analysis are needed to ensure accurate and precise population estimates from such monitoring efforts that can be compared across time and space. In this chapter, we review methods used for surveying and analyzing data on the three primate species occurring in Mexico and evaluate the eligibility of hierarchical modeling for such survey data. We conclude by arguing for the increased use of hierarchical models for these cryptic species.

6.2 Survey Methods for Spider and Howler Monkeys

Various survey methods have been used to infer the occupancy, abundance, or density of spider and howler monkeys, including line- and strip-transect sampling, point-transect sampling, recce walks, complete counts, lure counts using playback recordings, acoustic triangulation, passive acoustic monitoring, arboreal camera trapping, and drone surveys (Table 6.1; see Spaan et al. in review). Information on the presence of spider and howler monkey species can also be gathered indirectly through interviewing local people (Calixto-Pérez et al. 2018; Shedden et al. 2022) and the emergence of open-access biodiversity databases such as the Global Biodiversity Information Facility (www.GBIF.org) allows for larger-scale studies that make use of preexisting presence data (Vidal-García and Serio-Silva 2011). In the following sections, we selected two common traditional survey methods and two more recently developed survey methods for spider and howler monkeys to show the feasibility of combining them with hierarchical modeling approaches.

6.2.1 Examples of Traditional Survey Methods for Spider and Howler Monkeys: Line-Transect Sampling and Acoustic Triangulation

Line-transect sampling is the most commonly used method to estimate primate densities (i.e., the number of individuals or groups per unit area) in their natural habitat (Buckland et al. 2010; Campbell et al. 2016; Plumptre et al. 2013). The method consists of observers counting the number of individuals or groups of the species of interest detected while walking a continuous straight trail of a certain length (Plumptre et al. 2013). When applying a distance-sampling approach, certain detection is assumed only for animals located directly on the transect line, while detection probability decreases for animals located at increasing distances from the transect line (Buckland et al. 2015). Based on the number of detected animals and their perpendicular distance from the transect line, the density of individuals or groups can be estimated using a detection function or a cut-off width (as used during strip-transect or belt-transect sampling; Buckland et al. 2015). Sightings from line-

Table 6.1 Survey methods used for occurrence and abundance estimation of howler (*Alouatta* spp.) and spider monkeys (*Ateles* spp.) in Mexico (when available) and other countries

Survey method	Description	Example study for howler monkeys	Example study for spider monkeys
Camera traps	Use of remote photographic or video devices to detect species	Cudney-Valenzuela et al. (2021): *A. pigra*	Blake et al. (2010): *A. belzebuth*
Complete counts	Ground surveys covering the complete area of a predefined size, assuming all individuals present were detected	Galán-Acedo et al. (2021): *A. pigra, A. palliata*	NA
Database	Presence data based on publicly available datasets	Vidal-García and Serio-Silva (2011): *A. pigra, A. palliata*	Vidal-García and Serio-Silva (2011): *A. geoffroyi*
Drone surveys	Systematic aerial surveys using drones along transect lines or covering a predefined area	Kays et al. (2019): *A. palliata*	Spaan et al. (2019a): *A. geoffroyi*
Historic records	Use of specimen records and catalog entries of selected museums to gather presence data of species	Baumgarten and Williamson (2007): *A. pigra, A. palliata*	Ortiz-Martínez et al. (2008): *A. geoffroyi*
Interviews	Use of questionnaires or workshops to gather presence data of species from local informants or experts	Calixto-Pérez et al. (2018): *A. pigra, A. palliata*	Calixto-Pérez et al. (2018): *A. geoffroyi*
Line- or strip-transect sampling	Systematic ground surveys on transect lines	Anzures-Dadda and Manson (2006): *A. palliata*	Spaan et al. (2020): *A. geoffroyi*
Passive acoustic monitoring	Use of remote sound recording devices to detect species vocalizations	Do Nascimento et al. (2021): *A. caraya*	Hutschenreiter et al. (2022): *A. geoffroyi*
Playbacks	Auditory detection of animals by broadcasting recorded species calls to prompt a vocal response	Salcedo et al. (2014): *A. palliata*	Peck et al. (2010): *A. fusciceps*
Point-count sampling	Systematic ground surveys at selected points for a predetermined period	NA	Hutschenreiter et al. (2022): *A. geoffroyi*
Recce walks	Ground surveys on existing trails, no systematic search	Arroyo-Rodríguez et al. (2013): *A. pigra*	Ortiz-Martínez and Rico-Gray (2007): *A. geoffroyi*
Triangulation	Simultaneous ground surveys in person or using sound recording devices at multiple locations to determine the position of vocalizing animals	Estrada et al. (2004): *A. pigra*	Estrada et al. (2004): unsuccessful for *A. geoffroyi*

transect sampling can also be used to calculate encounter rates as the number of detected individuals or groups per unit distance or survey or to obtain presence/absence data per transect walk (Campbell et al. 2016). Such presence and count data can be combined with hierarchical modeling, which is useful when detection probability is expected to differ systematically between transect walks (e.g., when vegetation density varies across sites or when climatic conditions vary greatly across survey periods).

As howler monkeys emit intense vocalizations at specific times of the day, acoustic triangulation is another survey method traditionally used to determine howler monkey occupancy and group density (Estrada et al. 2004; Stoner 1994). Acoustic triangulation consists in the establishment of at least three listening posts covering a survey area at which observers note the time and compass direction of a call (Brockelman and Ali 1987). By combining the information from the listening posts, the location of the calling animals can be determined. Then, population density can be estimated from the number of calling individuals or groups per survey area as the total area at which calls can be detected by at least two listening posts (Brockelman and Ali 1987; Gilhooly et al. 2015). To obtain accurate population density estimates using this method, it is crucial to perform surveys over a period of time that ensures that each individual or group inhabiting the survey area calls at some point and hence is detected. Alternatively, a correction factor accounting for noncalling animals can be incorporated into the statistical analysis (Cheyne et al. 2008; Gilhooly et al. 2015). Hierarchical modeling could aid with the latter by accounting for the detection heterogeneity of calling subjects by modeling call detectability as a binomial distribution (detected or not detected; Kéry and Royle 2016), but we are not aware of a study that has done so yet. Although density estimates from triangulation can also be derived using distance-sampling approaches (Gilhooly et al. 2015), the use of hierarchical modeling such as N-mixture models might be superior given that sound transmission is affected by a variety of other factors apart from animal–observer distance (see next section).

6.2.2 *Examples of Novel Survey Methods for Spider and Howler Monkeys: Drones and Passive Acoustic Monitoring*

Recently, new survey methods for spider and howler monkeys have been developed to increase survey efficiency given that line-transect sampling for such low-density occurring species usually results in high proportions of zero detections (Hutschenreiter et al. 2021; Plumptre et al. 2013). Drones can cover large survey areas in a short time and have become increasingly popular as a survey tool for a broad variety of species (Wich and Koh 2018). Kays et al. (2019) and Spaan et al. (2019a) were able to detect Geoffroy's spider monkeys and mantled howler monkeys using drones mounted with thermal cameras. The primates were detected based on the difference in reflectance between the animals' body temperature and the surface temperature of the forest canopy. Although accurate detection from thermal images can be problematic in forests where similarly sized arboreal mammal species coexist due to possible false-positive detections from species mix-ups (Kays et al. 2019), thermal imaging is a promising tool in abundance estimation of spider monkeys as individuals in large subgroups can be counted more accurately than from the ground (Spaan et al. 2019a). Abundance estimation for howler monkeys is likely to be equally successful using this survey method but has not been tested yet.

Counts from drone surveys can be used to obtain relative densities and encounter rates (Wich et al. 2016) and be combined with hierarchical modeling to obtain animal densities (Corcoran et al. 2020). The combination of drone surveys with distance-sampling approaches is rather challenging for arboreal animals as the probability of detecting an individual does not necessarily depend on its distance from the transect line but rather on its vertical position in the tree canopy and on technical factors such as flight altitude (Witczuk and Pagacz 2021) and ground-sampling distance (Bonnin et al. 2018). These technical factors can be easily incorporated in hierarchical abundance approaches such as N-mixture models (Corcoran et al. 2020). Alternatively, presence/absence data can be collected during drone surveys for spider (and possibly howler) monkeys using visual-spectrum red-green-blue (RGB) cameras (Kays et al. 2019; Spaan et al. 2022) instead of thermal cameras. Although many individuals are missed on RGB images because only animals located above the tree canopy are detected, this less cost-intensive survey method (compared to drone surveys using thermal imaging) is perfectly suitable to be combined with hierarchical modeling approaches such as occupancy modeling (Williams et al. 2017).

Based on the success of triangulation surveys for howler monkeys, passive acoustic monitoring is a promising survey method for the *Alouatta* genera. It has recently been applied to survey black-and-gold howler monkeys (*A. caraya*, Do Nascimento et al. 2021; Pérez-Granados and Schuchmann 2021) and successfully been tested for black howler monkeys (Hutschenreiter et al. 2023). Geoffroy's spider monkeys were also successfully surveyed using passive acoustic monitoring (Hutschenreiter et al. 2022; Lawson et al. 2023), despite the less intense nature of the species' vocal repertoire compared to that of howler monkeys. To conduct passive acoustic monitoring, autonomous recording units (ARUs) are used to capture sounds from the environment in a circular survey area around the ARU (Deichmann et al. 2018; Gibb et al. 2019). The acoustic information can then be analyzed for various purposes, such as the detection of a species by the presence of its vocalization in the acoustic recordings (Gibb et al. 2019). Passive acoustic monitoring is mostly used to obtain presence/absence data and therefore is frequently combined with occupancy modeling (Campos-Cerqueira and Aide 2016). Various techniques have also been developed for population density estimation depending on the information compiled (Marques et al. 2013; Pérez-Granados and Traba 2021; Thompson et al. 2010). For example, if distance estimation between a vocalizing animal and ARU is possible (e.g., based on Sound Pressure Level measurements of the recorded vocalization), distance-sampling approaches using point-transect protocols can be applied (Marques et al. 2013). Alternatively, vocal activity rates (i.e., the number of detected vocalizations during sampling time) can provide a relative density estimate (Thompson et al. 2010). However, density estimation from passive acoustic monitoring is a very recent development and has not been applied to any spider or howler monkey species surveys to date. The use of hierarchical models for analyzing acoustic data is beneficial because sound transmission is influenced by a variety of factors such as weather conditions (Huveneers et al. 2016) and anthropogenic background noise (Zwerts et al. 2021) that might also influence species' abundance or occupancy. Hierarchical models can include such factors independently as covariates affecting detection probability and as covariates affecting abundance or occupancy estimates without confounding these types of effects.

Since primate calls recorded during passive acoustic monitoring cannot be assumed to be independent detections (because various calls could stem from the same individual or from different individuals of the same group or subgroup), we recommend the use of occupancy and Royle–Nichols models that are based on presence/absence data in combination with this survey method. Alternatively, relative abundance estimates of howler monkeys can be obtained (Kéry and Royle 2016) based on the number of detected vocalizations, assuming that the vocal activity at a site increases with increasing species abundance (Thompson et al. 2010). This is the case for agonistic loud call detections from both black and mantled howler monkeys, as roaring males evoke vocal responses from males of neighboring groups (Briseño-Jaramillo et al. 2021; Ceccarelli et al. 2021). In contrast, the use of detected vocalization numbers to estimate relative abundance is not recommended for species with high degrees of fission–fusion dynamics such as spider monkeys because vocalization rates might reflect subgroup-spacing behavior rather than group size (Dubreuil et al. 2015; Spehar and Di Fiore 2013).

6.2.3 Detection Probability Based on the Behavioral Ecology of Spider and Howler Monkeys

When considering variables that potentially influence the probability to detect an animal, the behavioral ecology of the species of interest can provide valuable information. By accounting for animal movements, activity budgets, social behavior, habitat use, and their temporal variation, researchers can determine how and when to survey the species of interest, what factors may hamper detection, and whether assumptions are met for applying a particular data-analysis method. The following are a few examples of how the behavioral ecology of spider (*Ateles* spp.) and howler monkeys (*Alouatta* spp.) potentially impact detection probability during surveys and selection of data-analysis options.

Spider monkeys and howler monkeys are highly arboreal primates, which make them generally difficult to detect in the dense tropical forests they inhabit. As they spend most of their time in the upper canopy (Wallace 2008; Youlatos and Guillot 2015), leaf coverage often impedes visual detection from both the ground and the sky (Spaan et al. 2019a). In forests where leaf coverage changes substantially throughout the year, detection probability might vary between seasons. Spider monkeys are generally easier to detect when moving or feeding compared to when they are resting due to the additional visual cues (such as moving branches and tree crowns) and auditory cues (such as cracking of branches while traveling, fruit dropping sounds while feeding, and vocalizations) that aid in perceiving their presence. It is hence recommendable to survey spider monkeys during hours of elevated activity, typically during the morning and late afternoon (Di Fiore et al. 2008), when using a survey method that relies on such cues. Given their generally slow movements, howler monkeys are less detectable by visual cues than spider monkeys. However, the loud and low-frequency roaring of male howler monkeys can be heard up to large distances (Bergman et al. 2016; Da Cunha and Byrne 2006; Van Belle et al. 2014) making it fairly easy to determine their presence through auditory cues. These loud calls are emitted by either one or several individuals (Briseño-Jaramillo et al. 2017; Cornick and Markowitz 2002) in the early morning and late afternoon, making these the preferable survey periods for howler monkeys.

Spider monkeys live in multimale–multifemale groups (Schaffner et al. 2012) with a high degree of fission–fusion dynamics, resulting in the formation of subgroups that frequently change in size and composition (Aureli et al. 2008). Whereas this highly flexible component of their social system impedes accurate abundance estimation of spider monkey groups or individuals (Spaan et al. 2019b), it may facilitate the detection of group members dispersed in subgroups over wide areas (Ramos-Fernández et al. 2011) compared to species with a high degree of group cohesion (Spaan et al. in review). As subgroup number and size change in relation to food availability (Pinacho-Guendulain and Ramos-Fernández 2017), the detection probability of a spider monkey group may also change across seasons. When information is available on the feeding tree phenology of a surveyed area, it might thus be useful to add food abundance at a site as a numeric covariate for modeling spider monkey detection probability. When such information is not available, simply accounting for the time of a survey (e.g., by including Julian day or current season as a covariate) may perform equally well to explain variation in detection probability.

Howler monkeys live in multimale or unimale groups with several females and subadult offspring (Van Belle and Estrada 2006). Average group sizes and degree of fission–fusion dynamics differ between species, with mantled howler monkeys forming larger groups (6–23 individuals; Crockett and Eisenberg 1986) with a higher degree of fission–fusion dynamics (Dias and Luna 2006) than black howler monkeys (4–6 individuals; Crockett and Eisenberg 1986). As larger groups are generally easier to sight or hear, detection probabilities for different howler monkey species might differ even though the same survey method is used.

Home-range estimates for Geoffroy's spider monkeys vary greatly (Fedigan et al. 1988; Ramos-Fernández and Ayala-Orozco 2003; Chaves et al. 2011) and can be as small as 5 ha (Ramos-Fernández et al. 2013) and as large as 304 ha (Asensio et al. 2012) reflecting not only the impact of different ecological factors but also methodologically induced variability in home-range estimates (Boyle 2021). Home-range estimates for howler monkeys are smaller than for spider monkeys (6–75 ha for *A. palliata*; 1–33 ha for *A. pigra*; Arroyo-Rodríguez et al. 2015), and home-range sizes decrease with increasing group density in a forest (Fortes et al. 2015). Standardizing sampling units for spider and howler monkey surveys (e.g., length of line transects, the distance between remote sensors, or area covered by drone surveys) based on home-range sizes can thus be ambiguous, but the interdependence of sampling units does not necessarily impede accurate occupancy estimation, as long as sites are selected randomly (MachKenzie and Royle 2005).

6.3 Current Use of Survey and Data-Analysis Methods for Mexican Primate Species

Despite the variety of survey methods used for spider and howler monkeys (Table 6.1) and the feasibility of combining them with hierarchical modeling, hierarchical modeling is still not frequently applied to data from primate surveys. We conducted a literature review to evaluate the use of survey methods, data-analysis methods, and response variables to assess occurrence, abundance, and group composition patterns in any of the three Mexican primate species since 2002, the year in which the first study on hierarchical modeling of unmarked populations was published (MacKenzie et al. 2002).

6.3.1 Literature Review

In May 2022, we conducted a search in Scopus for literature in English using a variety of terms related to primate surveys in Mexico (*Primate** OR *monkey** OR *Ateles* OR *Alouatta* AND *Mexico* OR *Oaxaca* OR *Chiapas* OR *Yucatan* OR *Quintana Roo* OR *Tabasco* OR *Campeche* OR *Veracruz* AND *survey* OR *density* OR *distribution* OR *abundance* OR *transect** OR *occurrence* OR *presence* OR *rang** OR *habitat* OR *space use* OR *population* OR *encounter* OR *absence* OR *occupancy*). Scopus was selected as it is one of the most extensive databases for literature published from a wide range of journals after 1995 (Falagas et al. 2008). We included original research articles and book chapters reporting previously unpublished data. To check for any work on hierarchical modeling published in Spanish that might have been missed due to the use of Scopus, we also scanned the available literature in Spanish using Google Scholar. However, we did not find any additional research using hierarchical modeling to analyze data from Mexican primate surveys.

We found 342 studies that matched our criteria of the Scopus search. As a first step, we excluded results by title and abstract that were review articles and book chapters reporting previously published data, studies not carried out in Mexico, studies that reported no survey data, or no data on primate species. Of the remaining 39 results, we further excluded: two studies that tested methodological aspects of surveys instead of collecting survey data, one study that predicted future trends in distribution under different climate change scenarios, one study that included survey data from outside Mexico, two studies with no or minimal information on how surveys were conducted, one study on hybrid species, and four studies that were published before 2002. These exclusions resulted in 28 studies published between January 2002 and May 2022 reporting data from Mexican primate surveys. We additionally included one research article published in July 2022 by us and one book chapter known to us that was not found during the literature search. Therefore, we considered a total of 30 studies for the analyses (Table 6.2). We extracted information on the publication year, the species surveyed, the sites where surveys were carried out, the survey methods, data-analysis methods, and response variable (s) derived from survey data for each of the 30 studies.

6.3.2 Locations of Mexican Primate Surveys

Surveys on primate species were carried out at various sites in all Mexican states of their known geographic distribution (Fig. 6.2). Four studies included surveys at multiple sites (leading to a total of 39 surveys), and six studies reported data on broader regions such as all of Southeastern Mexico, the Yucatan Peninsula, and the states of Campeche and Oaxaca. The most common sites were *Los Tuxtlas Biosphere Reserve* in Veracruz ($n = 4$ studies), *Palenque National Park* in Chiapas ($n = 4$), *Lacandona forest* in Chiapas ($n = 4$), and the *Uxpanapa valley* in Veracruz (n = 4). Together, these studies accounted for about 41% of all surveys (out of the 39 surveys in total; Fig. 6.2). Of the 30 studies, 10 reported data on *Alouatta palliata*, 20 on *Alouatta pigra,* and 13 on *Ateles geoffroyi* (11 studies reported data on more than one species).

6.3.3 Survey and Data-Analysis Methods Used in Mexican Primate Surveys

Nine methods were used to survey the three Mexican primate species' populations (Table 6.2 and Fig. 6.3). In 7 of the 30 studies, multiple survey methods were used and results were combined (Table 6.2). Recce walks were the most frequently reported survey method ($n = 13$ studies), followed by complete counts ($n = 7$) and line- or strip-transect sampling ($n = 6$). Whereas survey methods such as line-transect sampling, recce walks, interviews, and gathering information from historic records and databases were applied to all three species, four methods were used only

Table 6.2 Studies selected for the literature review

Source	Authors	Year	Species	Survey methods	Data-analysis method	Study ID
Scopus	Estrada et al.	2002	*A. pigra*	Triangulation	BPT	1
Scopus	Estrada et al.	2002b	*A. pigra*	Triangulation	Descr	2
Scopus	Fernández et al.	2003	*A. pigra*, *A. geoffroyi*	Recce walks, Interviews	Descr	3
Scopus	Estrada et al.	2004	*A. pigra*, *A. geoffroyi*	Triangulation, Recce walks	Descr	4
Scopus	Cristóbal-Azkarate et al.	2005	*A. palliata*	Complete count	MLR	5
Scopus	Anzures-Dadda & Manson	2006	*A. palliata*	Strip-/Line-transect sampling	GLMM	6
Additional	Serio-Silva et al.	2006	*A. pigra*, *A. geoffroyi*	Strip-/Line-transect sampling	Descr	7
Scopus	Baumgarten & Williamson	2007	*A. palliata*, *A. pigra*	Historic records, database, recce walks	Descr	8
Scopus	Ortiz-Martínez & Rico-Gray	2007	*A. geoffroyi*	Recce walks	Descr	9
Scopus	Arroyo-Rodríguez et al.	2008	*A. palliata*	Complete count	GLMM	10
Scopus	Pozo-Montuy et al.	2008	*A. pigra*	Recce walks	BPT	11
Scopus	Ortiz-Martínez et al.	2008	*A. pigra,* *A. geoffroyi*	Historic records, interviews, recce walks	ENM	12
Scopus	Urquiza-Haas et al.	2009	*A. pigra,* *A. geoffroyi*	Interviews	MLR	13
Scopus	Bonilla-Sánchez et al.	2010	*A. pigra*	Complete count	MLR	14
Scopus	Pozo-Montuy et al.	2011	*A. pigra*	Recce walks	GLMM	15
Scopus	Vidal-García & Serio-Silva	2011	All three	Interviews, database, recce walks	ENM	16
Scopus	Arroyo-Rodríguez et al.	2013	*A. pigra*	Recce walks	MLR	17
Scopus	Puig-Lagunes et al.	2016	*A. palliata*	Recce walks	GLMM	18
Scopus	Ortiz-Lozada et al.	2017	*A. palliata*	Strip-/line-transect sampling	Descr	19
Scopus	Calixto-Pérez et al.	2018	All three	Interviews, database	ENM	20

(continued)

Table 6.2 (continued)

Source	Authors	Year	Species	Survey methods	Data-analysis method	Study ID
Scopus	Galán-Acedo et al.	2019	*A. geoffroyi*	Recce walks	GLMM	21
Scopus	Arce-Peña et al.	2019	*A. pigra*	Recce walks	MLR	22
Scopus	Klass et al.	2020	*A. pigra*	Complete count	RA	23
Scopus	Alcocer-Rodríguez et al.	2020	*A. palliata*	Complete count	MLR	24
Scopus	Klass et al.	2020b	*A. pigra*	Complete count	BNPT	25
Scopus	Spaan et al	2020	*A. geoffroyi*	Strip-/Line-transect sampling	GLMM	26
Scopus	Spaan et al.	2021	*A. pigra,* *A. geoffroyi*	Strip-/Line-transect sampling	Descr	27
Scopus	Galán-Acedo et al.	2021	*A. palliata*, *A. pigra*	Complete count	GLMM	28
Scopus	Shedden et al.	2022	*A. pigra,* *A. geoffroyi*	Recce walks	GLMM	29
Additional	Hutschenreiter et al.	2022	*A. geoffroyi*	Point-count sampling, PAM	HM	30

Notes. Year = Year of publication (first published online). Survey methods and data-analysis methods correspond to descriptions in Tables 6.1 and 6.4. Study ID corresponds to IDs in Fig. 6.2. *BPT* Bivariate parametric test, *Descr* descriptive statistics or not reported, *MLR* multiple linear regression (general linear models), *GLMM* generalized linear (mixed) models, *ENM* ecological niche modeling, *RA* redundancy analysis, *BNPT* bivariate nonparametric test, *HM* hierarchical modeling

to survey one to two species: Complete counts were not applied to survey Geoffroy's spider monkeys, and triangulation was not used to survey mantled howler monkeys. Passive acoustic monitoring and point-count sampling were only used to survey Geoffroy's spider monkeys.

Data-analysis methods used in the 30 studies are described in Table 6.3. Most studies used generalized linear (mixed) models (GLMM: $n = 8$) or reported descriptive statistics and population density estimates without explicitly mentioning the calculation method used (Descriptive or not reported: $n = 8$). Only one study used a hierarchical modeling approach by running Royle–Nichols models. Whereas the use of descriptive statistics and bivariate parametric tests was predominant before 2010, the use of GLMMs and ecological niche modeling became prominent within the past 10 years (Fig. 6.4).

The combinations of survey methods and data-analysis methods used for all species are illustrated in Fig. 6.5. The most common combinations were the use of recce walks to run multiple linear regressions or GLMMs.

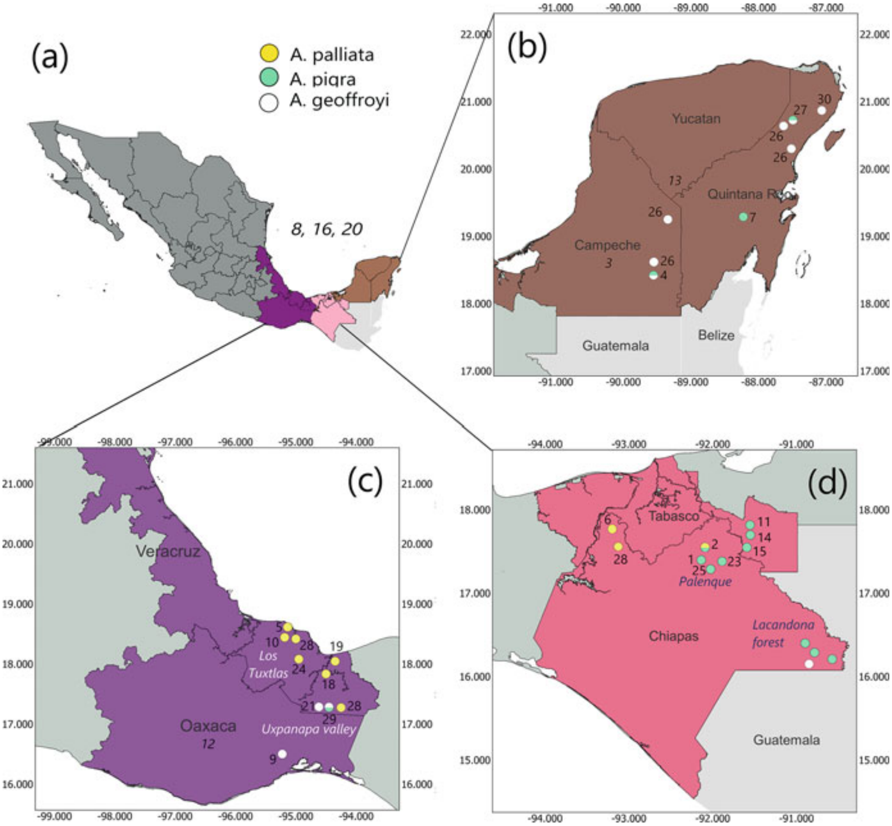

Fig. 6.2 Map of primate surveys carried out in Mexico since 2002. Highlighted areas in (**a**) show the Mexican multistate regions where surveys took place, and (**b**–**d**) show the specific locations where survey studies were carried out in each area. Numbers coincide with study IDs from Table 6.2. Bicolored circles indicate more than one species was surveyed in the same study. Study IDs in (**a**) refer to nationwide surveys. Broad-scale surveys also include one survey of the Yucatan Peninsula (*13*), one in the state of Campeche (*3*), and one in the state of Oaxaca (*12*)

6.3.4 Response Variables Used in Mexican Primate Surveys

Survey data were used to calculate from one to nine response variables per study and species. As studies evaluate different aspects of the species' population ecology, we grouped response variables into five types: abundance of individuals, group composition, abundance of groups, species presence/absence, and others (Table 6.4). Whereas abundance of individuals was the most common type of response variable for surveys on the black howler monkey (42%, $n = 15$ response variables), presence/absence-related outcomes were most reported for the mantled howler monkey (47%, $n = 9$). The abundance of individuals (27%, $n = 6$) and presence/absence-related

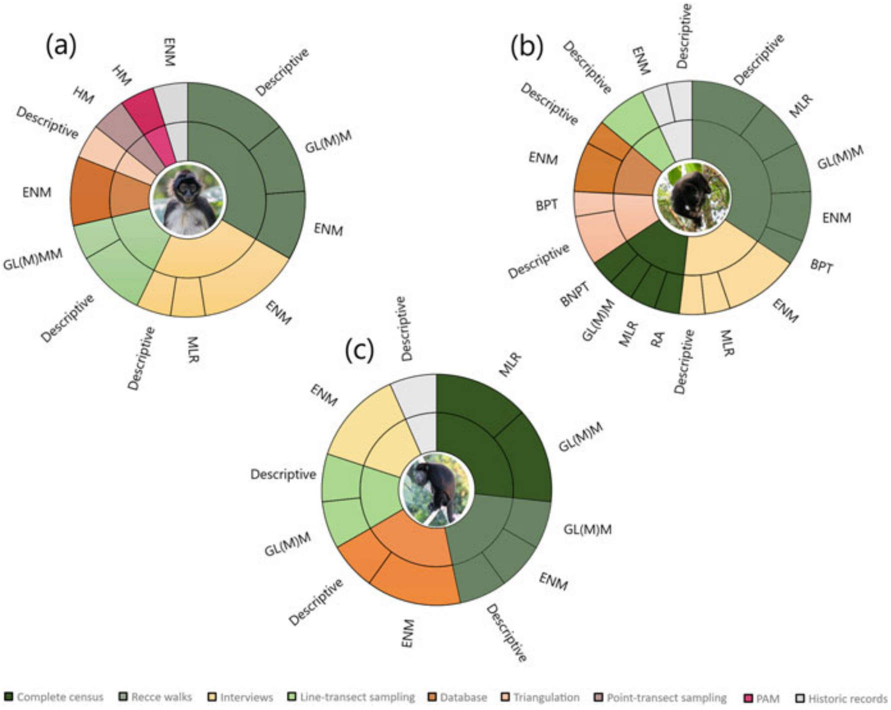

Fig. 6.3 Survey methods (the inner circle) and corresponding data-analysis methods (outer circle) were reported for studies on (**a**) *Ateles geoffroyi,* (**b**) *Alouatta pigra*, and (**c**) *Alouatta palliata*. Descriptive Descriptive statistics or not reported, HM Hierarchical modeling, GL(M)M Generalized linear (mixed) models, ENM Ecological niche modeling (see Table 6.3 for details on data-analysis methods). When multiple data-analysis methods were used in the same study, we report the statistical approach with the highest complexity among them (see Table 6.3 for the degree of complexity)

outcomes (27%, $n = 6$) were the most reported response variables for Geoffroy's spider monkey (Table 6.4).

Types of response variables were combined with several data-analysis methods across species (Fig. 6.5). Response variables measuring the abundance of individuals and group composition were mostly combined with descriptive statistics (12%, $n = 7$ combinations), whereas response variables based on species presence/absence data were more broadly combined with data-analysis methods including ecological niche modeling, GLMMs and descriptive statistics (15%, $n = 9$; Fig. 6.5).

Table 6.3 Data-analysis methods used for data derived from Mexican primate surveys

Data-analysis method category	Details of the specific methods used in the 30 studies	Degree of complexity (criterion for the degree)
Descriptive or not reported	No statistical inference or distance-sampling approach used; if density estimates are reported, no information about how they were calculated	Low (no inferential statistics)
Bivariate non-parametric test	Mann–Whitney U-test, Kruskal–Wallis test and Spearman rank correlation	Low (one dependent and one independent factor)
Bivariate parametric test	T-test and bivariate linear regression, assuming normal error distribution of response variable	Low (one dependent and one independent factor)
Multiple linear regression	General linear models, i.e., multiple (including stepwise) regression models assuming normal error distribution of response variables	Intermediate (one dependent and multiple independent factors)
Redundancy analysis	Extension of multiple linear regression to analyze variation in multiple response variables	Intermediate (multiple dependent and independent factors)
GLMM	Generalized linear models or generalized linear mixed models, i.e., assuming non-normal error distribution of the response variable	High (one dependent and multiple independent factors, possibility to include random effects)
Ecological niche modeling	Correlative model of presence data and climatic parameters to predict species habitat suitability	High (one dependent and multiple independent factors, specifically developed for modeling species distribution)
Hierarchical modeling	Conditionally related set of generalized linear models	Highest (two dependent and multiple independent factors, linking sets of models through conditional probabilities)

6.4 Discussion

In our literature review, we found 30 studies reporting survey data on Mexican primate species that were published between 2002 and 2022. The black howler monkey was the most often surveyed species followed by Geoffroy’s spider monkey and the mantled howler monkey. Most surveys were conducted at a few sites in the states of Chiapas and Veracruz. Despite a great variety of methods used to collect and analyze data from Mexican primate surveys, we found only one study that used hierarchical modeling for data analysis. GLMMs and descriptive statistics were the most common data-analysis methods overall, although there appears to be a trend toward using more complex data-analysis methods over time. In most studies, response variables related to the individual abundance of a species were reported, followed by measures of presence/absence-related outcomes and measures of group composition.

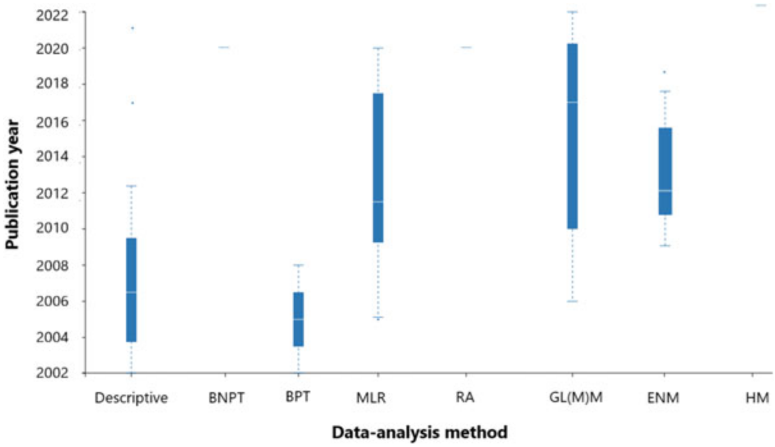

Fig. 6.4 Data-analysis methods used in the 30 reviewed studies plotted by their year of publication. When multiple data-analysis methods were used in the same study, we report the statistical approach with the highest complexity among them (see Table 6.3 for the degree of complexity). Boxplots show minimum and maximum values (lower and upper whiskers), first and third quartile (lower and upper box limits), medians (white lines), and outliers (dots) for each data-analysis method. Methods used in only one study are represented by a single line corresponding to the publication year. Abbreviations for data-analysis methods correspond to those used in Table 6.2

Notably, the total number of surveys on Mexican primate populations since 2002 is small. This, in part, is certainly the result of limiting our literature review to Scopus, which includes less gray literature than databases such as Google Scholar (Calver et al. 2017). Hence, we probably missed unpublished work such as dissertations, reports for funding bodies and by governmental agencies and NGOs, and literature that was published in regional/national journals and IUCN specialist group journals. This was intentional as our aim was not to conduct an extensive systematic review but to create an overall picture of the main methods used to survey Mexican primates. Still, we point out that presumably more surveys were conducted on Mexican primates than reported in this chapter, including surveys from studies we excluded, e.g., those that used data from inside and outside Mexico in the same analysis or lacked information on survey methodology, as well as multispecies studies that included data on Mexican primate species but report results at the community level (e.g., Cudney-Valenzuela et al. 2021). As the latter type of studies was not picked up by our search strategy (i.e., using keywords related to Mexican primates specifically rather than to animal assemblages), we might have missed studies using hierarchical modeling for data on Mexican animal communities that included primate species.

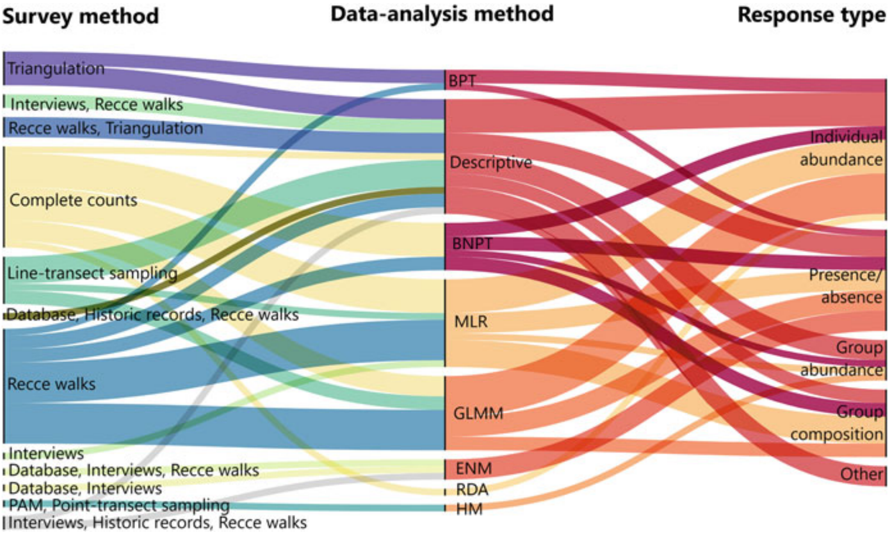

Fig. 6.5 Combinations of survey methods, data-analysis methods, and types of response variables used in the 30 studies (based on 57 data points as multiple types of data-analysis methods and response variables were used in 18 studies). Colored lines connect survey methods with the data-analysis methods and data-analysis methods with the types of response variables they were combined with. The thicker the line, the more often a specific combination of survey and data-analysis method or data-analysis method and type of response variable reported. Vertical black bars indicate which lines are connected to the respective survey method, data-analysis method, and type of response variable. The order of methods and response types was set to minimize overlap between lines for improved readability. Note that all data-analysis methods were included in the Figure, not only those of the highest complexity in a study

6.4.1 Survey Methods

We found recce walks to be the most common method to survey Mexican primate species since 2002 followed by complete counts and line-transect sampling, all consisting of observers detecting primates from the ground (Plumptre et al. 2013). Recce walks have no systematic search strategy, which makes the method more susceptible to bias from observer behavior (e.g., spending more time scanning more accessible areas or areas where the species is assumed to be present) than line-transect sampling, and is prone to bias from heterogeneity in detection probability (Campbell et al. 2016). In contrast, the use of complete counts assumes that all animals present in an area are detected during a survey (Plumptre et al. 2013; Campbell et al. 2016), making it unnecessary to control survey results for detection probability. This method is therefore preferable to recce walks, when feasible, i.e., when habitat type, animal behavior, observer experience, and survey effort allow for detection of all individuals present, as it is the case, e.g., for howler monkey surveys in small forest fragments (Klass et al. 2020a). Feasibility of complete counts, however, is often hampered in surveys of arboreal primate species given the low

Table 6.4 Types of response variables derived from data from Mexican primate surveys

Type of response variable	Specific response variables	Percentage of use (%)[a]		
		A. geoffroyi	*A. pigra*	*A. palliata*
Abundance of individuals	Individual encounter rates Individual density Number of individuals per group Number of individuals per sub-group Number of individuals per fragment	27	42	26
Group composition	Adult sex ratio Juvenile sex ratio Immature-to-female ratio Immature-to-adult ratio Infant-to-adult ratio Infant-to-female ratio Juvenile-to-infant ratio	14	19	16
Abundance of groups	Group density Number of groups at study site Subgroup density λ (average abundance at site)	18	11	11
Species presence/ absence	Naïve occupancy Naïve patch occupancy Presence or absence Presence probability Predicted distribution	27	22	47
Other	Area of distribution Habitat type Biomass	14	6	0

[a] The percentage of use was calculated out of the total number of types of response variables used in all studies for each of the three species

visibility in tropical forests, causing individuals to be missed due to imperfect detection (Spaan et al. 2017), and the high mobility of the animals in a vast space, causing individuals to be missed due to their temporary absence during the time of the survey (Plumptre et al. 2013; Dénes et al. 2015). Recently developed survey methods, such as drone surveys with thermal infrared cameras, can contribute to increasing the feasibility of complete counts by covering large survey areas with high detectability, but these methods are still in development for Mexican primates (Spaan et al. 2019a). Whether requirements are met to consider survey results as complete counts (also called “full counts,” “total count method,” or “complete census”) also depends on the definition of the term (which may differ between fields) and on the unit of observation (e.g., a focal patch or a specified sample area). It is vital to define the dependent variable to allow comparisons between studies. Note that the studies in our review report complete counts as surveys that cover entirely an area of predetermined size and assume all individuals present were detected.

Line-transect sampling is the preferred ground-survey method when requirements for total counts are not met (Campbell et al. 2016) as its standardized methodology allows for the application of data-analysis methods accounting for differences in detection probability (e.g., distance sampling; Buckland et al. 2010). However, in areas of challenging terrain or restricted accessibility, line-transect surveys may not always be logistically feasible. In such cases, point-transect sampling, camera-trap surveys, passive acoustic monitoring, or drone surveys might be more spatially flexible alternatives to detect primate species using standardized methodology.

The use of interviews as an indirect survey method is rare and mostly used in combination with other survey methods for presence-only data-analysis methods such as ecological niche modeling (Fig. 6.5). Local ecological knowledge is a valuable source of information and can provide accurate presence/absence data that coincide with results from direct survey methods such as ground surveys (Shedden et al. 2022). The potential for interviews as a survey method to be combined with data-analysis methods such as occupancy modeling should thus be further explored for its applicability to primate surveys. Recent studies have applied detectability measures to interview data to evaluate potential biases of presence/absence information based on local ecological knowledge. For example, Camino et al. (2020) estimated the probability of false-negative and false-positive detections of animals during interviews compared to information from camera-trapping and line-transect sampling, and Brittain et al. (2022) identified predictors of detection probability during interviews such as the time an informant spent in the forest. Once important predictors are identified, they can be incorporated into occupancy modeling with interview data to provide more accurate occupancy estimates. Like interviews, presence data from citizen science projects and open-access community science platforms (e.g., iNaturalist) are rich sources of information but are affected by bias (e.g., sightings might be clustered around touristic sites or cities). Modeling these sources of bias with hierarchical models (van Strien et al. 2013; Bird et al. 2014) can aid the addition of citizen science data into primate surveys. As such, interview and citizen science data will likely be increasingly used as a stand-alone survey method or in combination with other survey methods.

None of the studies reviewed used camera trapping or playbacks to survey Mexican primate species although these survey methods have been used at the community level (e.g., Cudney-Valenzuela et al. 2021) and for howler and spider monkeys outside of Mexico (Blake et al. 2010; Peck et al. 2010; Salcedo et al. 2014). Studies using novel survey methods for Mexican primate species are mostly aimed at improving methods to obtain accurate and precise population estimates (e.g., testing the use of drones: Spaan et al. 2019a, 2022) or were used to gather behavioral information (e.g., the use of camera traps to document terrestrial drinking behavior: Delgado-Martínez et al. 2021). Although these methodological studies indicate that novel survey methods will be applied to field surveys soon, traditional ground survey methods are still popular and will likely remain the standard in the near future across Mesoamerica. It is therefore important to promulgate how such traditional data-collection methods can be combined with recently developed data-analysis methods such as hierarchical modeling (Cavada et al. 2016).

Regardless of the method used (traditional or more recent survey methods), wide-scale surveys of Mexican primates have yet to take place. This is key, as although the national action plan for the conservation of Mexican primates (Oropeza Hernández and Rendón Hernández 2012) draws attention to the need to gain more information on their abundance and distribution, we found that most of the survey efforts in Mexico are focused on a few study sites. Knowledge gaps remain in many regions of the country, especially regarding the distributional limits of each of the three species and along the coast of the states of Oaxaca and Chiapas (Ortiz-Martínez et al. 2008).

6.4.2 *Data-Analysis Methods*

Although the use of descriptive statistics is still common practice in surveys on Mexican primate species, a trend toward the use of more complex multivariate data-analysis methods, predominantly GLMMs, over the past decade is evident from our literature review. GLMMs are a powerful tool to model Poisson-distributed count data or binomially distributed occurrence data, while accounting for the impact of a multitude of predictor variables (Bolker et al. 2008). A problem with using GLMMs to analyze survey data is that count or occurrence data might be biased by heterogeneity in detection probability across sites and survey periods if individuals are not detected with 100% certainty. Approaches such as model-based distance sampling (e.g., plot count models; Buckland et al. 2015), N-mixture models and hierarchical distance sampling (Kéry and Royle 2016) resolve this issue as these approaches correct count data for detection probability before modeling abundance as Poisson-distributed count data (i.e., before applying generalized linear modeling to count data). However, we found none of these approaches to have been applied to Mexican primate survey data.

Occupancy models and Royle–Nichols models are analogous options to correct for heterogeneity in detection probability before modeling occupancy or abundance based on occurrence data with a binomial error distribution (i.e., before applying generalized linear modeling to presence/absence data). We only found one study that applied Royle–Nichols models to the presence/absence data of Geoffroy’s spider monkeys (Hutschenreiter et al. 2022) and not a single study using occupancy modeling for any of the three species. Occupancy modeling is common practice in population monitoring studies for many other mammal species (Rivero and Spitale 2016) and can easily be applied to data from primate surveys (e.g., Johnson et al. 2020). Many of the studies included in our literature review collected presence/absence data and could easily have made use of occupancy modeling but instead used GLMMs (which is ideal when used in combination with complete counts, but not when there is heterogeneity in detection probability), only reported descriptive statistics, or used potentially inappropriate data-analysis methods (e.g., Bonilla-Sánchez et al. 2010) such as bivariate parametric tests or general linear models (Table 6.3 and Fig. 6.5). Both methods require the response variable to have normally distributed residuals, which is not the case for count and presence/absence data that usually follow Poisson and binomial error distributions (or derivates such as negative-binomial; Buckley 2015). When data are not corrected through, e.g., normalization approaches (as applied in Alcocer-Rodríguez et al. 2020; Arce-Peña et al. 2019; but see O'Hara and Kotze 2010), results from parametric data-analysis methods can lead to incorrect estimates of predictor variables (Buckley 2015) and should be used with caution in primate surveys. Given their limited informative power, the stand-alone use of descriptive statistics should be avoided when possible, considering the broad palette of data-analysis methods available for primate survey data.

The lack of use of distance-sampling approaches in the 30 studies obtained from our literature search might be caused partly by the need for a large number of sightings at a single site to accurately estimate population densities (Buckland et al. 2001), a number that is often unrealistic to obtain in surveys of primate species given the low densities at which most of these species occur (e.g., Spaan et al. 2020) and the usually low detection probabilities during surveys (Spaan et al. 2022). In contrast, the use of hierarchical modeling approaches is not encumbered by the need for a minimum number of sightings. Instead, survey effort can be increased to a reasonable extent if species occur at low densities (Guillera-Arroita et al. 2010) yet another reason we encourage the use of hierarchical modeling.

Despite the existence of hierarchical modeling for the past two decades, our literature review revealed that its widespread application to analyzing survey data on Mexican primates has yet to take place. Statistical approaches can only make their way into survey design when (1) these approaches are known, and (2), sufficient training is provided to implement them. For the former, attention needs to be drawn to the power and usefulness of a novel approach, such as through the release and dissemination of works like the present book. For the latter, the provision of capacity-building options among practitioners is crucial. Given the existing mismatch between the amount of available literature on hierarchical modeling and the frequency of its use with data from Mexican primate surveys, we emphasize the need for both attention-raising and training opportunities. Ecological statistics is a rapidly advancing field (Mundry 2019; Anderson et al. 2021), which sometimes makes it difficult to distinguish between statistical "fashion trends" that mainly aid in making a study more attractive for publication (Warton 2022), and approaches that provide valid solutions to existing problems and eventually become established research tools. In this chapter, we aimed to show that hierarchical modeling is such a powerful approach by arguing the various ways it can be advantageously used to survey data of spider and howler monkeys as well as of other primate and arboreal mammal species across Mesoamerica and South America.

6.4.3 Response Variables

We found the abundance of individuals to be the most common type of response variable calculated from survey data on Mexican primates. When the degree of fission–fusion dynamics is high to moderate, such as in spider monkeys (Aureli et al. 2008) and some populations of mantled howler monkeys (Dias and Luna 2006), reporting outcomes based on individual sightings is useful as subgroups of the same group can be widely spaced and vary in number and size depending on current food availability (Pinacho-Guendulain and Ramos-Fernández 2017; Spaan et al. 2019b). Hence, the size and composition of a sighted subgroup does not reveal any information about the group size and composition, and the number of sighted subgroups might be more related to seasonal food availability than to the actual group size. We, therefore, recommend the use of individual encounter rates or densities rather than subgroup size or subgroup density estimates for populations that form subgroups (i.e., a high to moderate degree of fission–fusion dynamics). Alternatively, the use of presence/absence data in hierarchical models can provide reliable estimates of occupancy and relative abundance when populations form subgroups. Royle–Nichols modeling might be more suitable than occupancy modeling in this case as it assumes heterogeneity in species abundance within sampling areas (Royle and Nichols 2003), which might better model the distribution of multiple primate groups and subgroups at a site (Hutschenreiter et al. 2022).

After individual abundance estimates and presence/absence-related outcomes, measures of group composition were the most commonly calculated response variables. To accurately estimate group composition and demography, researchers need to ensure that detection probability is consistent across individuals in the group. This is not always the case as, e.g., young might be missed easier than adult individuals (as shown for spider monkeys: Spaan et al. 2017), leading to biased group size and composition estimates. This is particularly problematic in two instances: (1) when comparing group size across sites or over time and (2) when calculating group composition ratios (e.g., young-adult female ratios), which provide important information on the reproductive and, therefore, conservation status of a population. To overcome biased estimates, it might be feasible to calculate detection probabilities separately for different age and sex categories of individuals (e.g., adults versus young or females versus males) and correct individual counts in each category before calculating corresponding ratios (e.g., young-adult female ratio). To our knowledge, no study on primate surveys has put such an approach to the test yet.

6.5 Conclusions

Our literature review revealed that, to date, the use of hierarchical modeling is still underrepresented in surveys on Mexican primate species, despite having been developed two decades ago and having been applied to surveys of many other mammal species. Besides distance sampling, hierarchical modeling provides the only approach to incorporate detection probability into estimates of species abundance, but in contrast to distance sampling, it can do so in a much more flexible way in combination with any type of traditional or novel survey method. Moreover, hierarchical modeling based on presence/absence data can overcome sampling bias due to high degrees of fission–fusion dynamics. We, therefore, emphasize the suitability of hierarchical modeling for Mexican and other primate surveys, and advocate for capacity building to implement this data-analysis method in field surveys.

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Chapter 7
Abundance, Density, and Occupancy of Ungulates in the Maya Forest: A Review

Eduardo J. Naranjo, Rafael Reyna-Hurtado, Fredy Falconi-Briones, and Wilber Evan Martinez

Abstract In this chapter, we present a review of all publications available and unpublished information of our own on both hierarchical and nonhierarchical estimates of the abundance, density, and habitat occupancy of native ungulate populations in the Greater Maya Forest, which is shared by southeastern Mexico, Northern Guatemala, and Belize. The white-lipped peccary (*Tayassu pecari*) and the collared peccary (*Pecari tajacu*) have been the most frequent objects of study within protected areas in this region, followed by Baird's tapir (*Tapirus bairdii*), white-tailed deer (*Odocoileus virginianus*), red brocket deer (*Mazama temama*), and Yucatan brown brocket deer (*M. pandora*). Occupancy and density assessments for all species are still scarce compared to population abundance. More information on the abundance, density, and occupancy of all species, but particularly the red brocket deer and the Yucatan brown brocket deer, is needed outside the largest protected areas in the Maya Forest.

Keywords Mazama · Odocoileus · Pecari · Tapirus · Tayassu

7.1 Introduction

The Greater Maya Forest constitutes one of the most important stronghold habitats for tapirs, peccaries, and red brocket deer in Mexico and Central America, and encompasses the entire distribution range of the Yucatan brown brocket deer (Weber 2005; Naranjo et al. 2015; Gallina-Tessaro 2019; Reyna-Hurtado and Sánchez-

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Fig. 7.1 View of the Peten Forest in Tikal National Park, northern Guatemala. (Photograph by Eduardo J. Naranjo)

Pinzón 2019; Thornton et al. 2020). It is the largest tract of rainforest in the Neotropics north of the Amazon (Nations et al. 1998). A formerly continuous block of tropical forest (from deciduous to evergreen) across southeastern Mexico, northern Guatemala, and Belize, this region has been the territory of the ancient and the modern Maya peoples for over 2000 years (Rodstrom et al. 1998; Fig. 7.1). The great biological, hydrological, and cultural richness of the Maya Forest has attracted colonists, researchers, and tourists for a long time (Ford and Nigh 2015). Nonetheless, the region has faced high rates of deforestation and forest fragmentation (ca. 80,000 ha/year; Nations et al. 1998) resulting from human population growth and land use change for logging, farming, and beef production (Bray et al. 2008).

The governments of Belize, Guatemala, and Mexico have established numerous protected areas across the Maya Forest to safeguard biodiversity, among which large biosphere reserves (e.g., Calakmul, Lacantun, Maya, Montes Azules, and Sian Ka’an), national parks (e.g., Chiquibul, Laguna del Tigre, Mirador-Rio Azul, Sierra del Lacandon, and Tikal), wildlife sanctuaries (e.g., Cockscomb Basin), and forest reserves (e.g., Columbia River and Mountain Pine Ridge) stand out (CONAP 1999; Meerman 2005; CONANP 2022). These protected areas constitute the core habitat of native mammals, especially ungulates, in the region (Fig. 7.2). However, there are still many community lands (i.e., indigenous territories, ejidos, and cooperatives) and large private properties sheltering important populations of deer, peccaries, and tapirs. Some of those populations outside preserves are under local management or protection, but many others are hunted with little or no control (Jorgenson 1998; Naranjo et al. 2015).

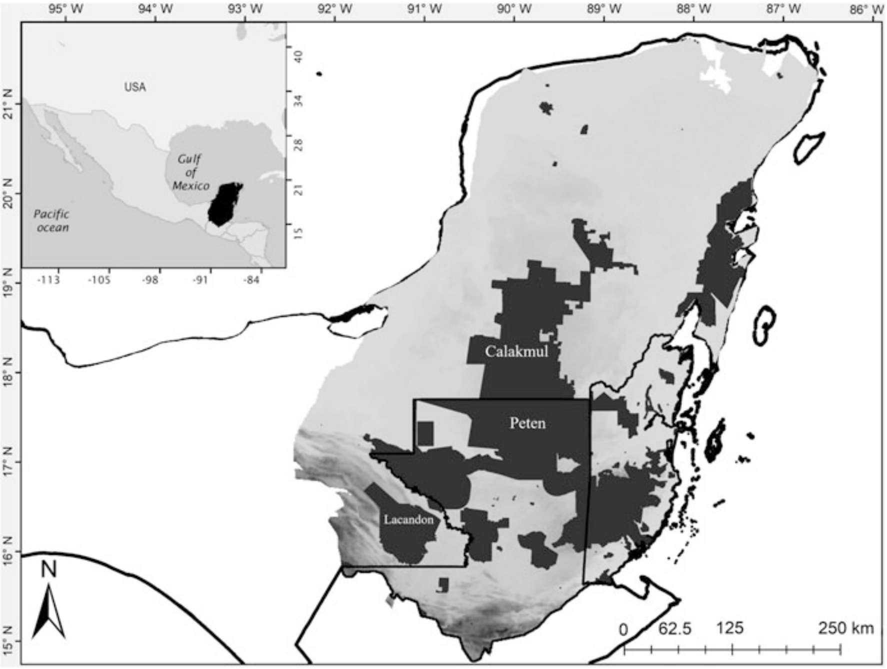

Fig. 7.2 Main study regions of native ungulates in the Grater Maya Forest. Black areas indicate the largest protected areas

The six ungulate species present in the Maya Forest are Baird's tapir (*Tapirus bairdii*), white-lipped peccary (*Tayassu pecari*), collared peccary (*Dicotyles tajacu*), red brocket deer (*Mazama temama*), Yucatan brown brocket deer (*M. pandora*), and white-tailed deer (*Odocoileus virginianus*) (Gallina-Tessaro 2019). Baird's tapir is listed as endangered in Mexico (SEMARNAT 2010), Guatemala (CONAP 2021), and globally (García et al. 2016), while the white-lipped peccary is threatened in the whole Mesoamerican region (Thornton et al. 2020). The Yucatan brown brocket deer is threatened in Guatemala and Belize (CONAP 2021; Meerman 2005), while the red brocket deer is listed as threatened only in Guatemala (CONAP 2021). The collared peccary and the white-tailed deer are not globally threatened, but some local populations may be at risk because of habitat loss and poaching (CONAP 2021). These two species are considered generalists and tolerant of hunting in the Maya Forest (Reyna-Hurtado and Tanner 2007; Naranjo and Bodmer 2007; Briceño et al. 2016; Moreira et al. 2019a; Falconi-Briones et al. 2022). In contrast, the two brocket deer species are forest specialists (Tejeda-Cruz et al. 2009; Gallina-Tessaro et al. 2019). Baird's tapir and the white-lipped peccary are far more sensitive to forest fragmentation and heavy hunting pressure than the other ungulates in this region (Naranjo and Bodmer 2007; Reyna-Hurtado et al. 2010; Moreira et al. 2019b; Naranjo 2019; Falconi-Briones et al. 2022). The purpose of this chapter was to analyze the state of current knowledge on the relative abundance, density, and occupancy of wild ungulates in the Grater Maya Forest based on all publications available and unpublished estimates of the authors.

7.2 Methods

We did searches for any documents containing information on the abundance, density, and occupancy of native ungulate species (deer, peccaries, and tapirs) in the Grater Maya Forest of southeastern Mexico, Belize, and northern Guatemala. Our searches were done by using the Web of Science, Scopus, Google Scholar, and Google websites with the following keywords: *ungulate*, *brocket deer*, *peccary*, *tapir*, *white-tailed deer*, *Mazama*, *Odocoileus*, *Tayassu*, *Tapirus*, *Pecari*, AND *Maya Forest*, *Yucatan Peninsula*, *southeast Mexico*, *Guatemala*, *Belize*, *Campeche*, *Chiapas*, and *Quintana Roo*. In this way, we retrieved a total of 57 documents, of which 34 met our criteria of containing estimates of abundance, density, and/or occupancy of one or more of our focal species within the boundaries of the Greater Maya Forest using either hierarchical or nonhierarchical approaches.

7.3 Results

The 34 documents that met our criteria were published or finalized between 2001 and 2022. Fifteen (44.1%) included information on the white-lipped peccary, 13 (38.2%) on the collared peccary, 12 (35.3%) on Baird's tapir, 11 (32.4%) on white-tailed deer, and 10 (29.4%) on brocket deer (*Mazama* spp.) (Fig. 7.3). Twenty

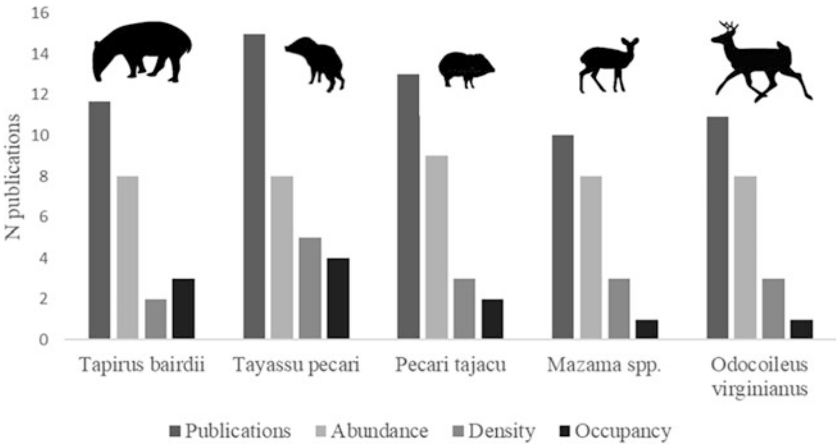

Fig. 7.3 Number of publications on the abundance, density, and occupancy of native ungulates in the Greater Maya Forest

Table 7.1 Abundance, density, and occupancy estimates of Baird's tapir (*Tapirus bairdii*) in the Maya Forest

Study site	Abundance/density/occupancy	Source
Lacandon Forest, Mexico	0.2 ind/km^2 26.1 tracks/100 km	Bolaños and Naranjo (2001)
Lacandon Forest, Mexico	0.5 sightings/100 km and 14.5 tracks/100 km (hunted sites); 1.22 sightings/100 km and 27.6 tracks/100 km (unhunted sites)	Naranjo and Bodmer (2002)
Lacandon Forest, Mexico	0.05 ind/km^2 (hunted sites); 0.24 ind/km^2 (unhunted sites)	Naranjo and Bodmer (2007)
Calakmul Forest, Mexico	42 tracks/100 km (hunted sites); 3 tracks/100 km (unhunted sites)	Reyna-Hurtado and Tanner (2007)
Lacandon Forest, Mexico	57.7 tracks/100 km	Tejeda-Cruz et al. (2009)
Yucatan Peninsula, Mexico	Occupancy rate = 0.12	Urquiza-Haas et al. (2009)
Calakmul Forest, Mexico	37.6 photos/1000 camera-days; 148 tracks/100 km	Pérez-Cortez (2011)
Calakmul Forest, Mexico	17 photos/1000 camera-days; 33 tracks/100 km	Carrillo-Reyna et al. (2015)
Lacandon Forest, Mexico	10.8 photos/1000 camera-days; 0.76 sightings/100 km; 10.3 tracks/100 km	Falconi (2017)
Southeastern Mexico	0.03–0.45 ind/100 km; 3.8–37.6 photos/1000 camera-days	Naranjo (2018)
Runaway Creek, Belize	Naïve occupancy = 85.7%; occupancy prob = 0.97; detection prob = 0.14	Martínez et al. (2021)
Lacandon Forest, Mexico	Occupancy prob = 0.50	Falconi-Briones et al. (2022) and Falconi et al. (unpublished data)
Calakmul Forest, Mexico	Occupancy prob = 0.73 (2014), 0.83 (2020); detection prob = 0.10 (2014), 0.26 (2020)	Reyna-Hurtado et al. (unpublished data)

(58.8%) of those surveys included estimates of relative abundance, while 10 (29.4%) presented densities, and only 6 (17.6%) reported occupancy by one or more ungulate species (Fig. 7.3). Most of the surveys (n = 29; 85.3%) were conducted in the Mexican portion of the Maya Forest, while only 3 and 1 were done on the Guatemalan and the Belizean sides, respectively (Tables 7.1, 7.2, and 7.3). It is interesting to note that hierarchical methodologies were applied in only 12 (35.3%) of the studies reviewed, and over half of them (n = 7) were focused on density estimates

Table 7.2 Abundance, density, and occupancy estimates of white-lipped peccary (*Tayassu pecari*) and collared peccary (*Pecari tajacu*) in the Maya Forest

Species	Study site	Abundance/density/occupancy	Source
T. pecari	Lacandon Forest, Mexico	3.8 ind/km^2; 9.4 tracks/100 km	Bolaños and Naranjo (2001)
T. pecari	Peten Forest, Guatemala	9.6 ind/km^2	Novack et al. (2005)
T. pecari	Lacandon Forest, Mexico	7.9 ind/km^2 (unhunted sites); 1.1 ind/km^2 (hunted sites)	Naranjo and Bodmer (2007)
T. pecari	Calakmul Forest, Mexico	8 tracks/100 km (hunted sites); 24 tracks/100 km (unhunted sites)	Reyna-Hurtado and Tanner (2007)
T. pecari	Lacandon Forest, Mexico	57.7 tracks/100 km	Tejeda-Cruz et al. (2009)
T. pecari	Yucatan Peninsula, Mexico	Occupancy rate = 0.04	Urquiza-Haas et al. (2009)
T. pecari	Calakmul Forest, Mexico	0.43 ind/km^2	Reyna-Hurtado et al. (2010)
T. pecari	Maya Forest Mexico	1.7–13.3 photos/1000 camera-days; 1.5–6.3 tracks/100 km	Naranjo et al. (2015)
T. pecari	Calakmul Forest, Mexico	10 photos/1000 camera-days (hunted sites), 18.4 photos/1000 camera-days (unhunted sites); 11 tracks/100 km (hunted sites), 16 tracks/100 km (unhunted sites)	Briceño et al. (2016)
T. pecari	Lacandon Forest, Mexico	80.9 photos/1000 camera-days; 18.9 ind/100 km; 7.6 tracks/100 km	Falconi (2017)
T. pecari	Peten Forest, Guatemala	0.33 ind/km^2; 44.9 photos/1000 camera-days (wet season), 257.1 photos/1000 camera-days (dry season)	Moreira et al. (2019b)
T. pecari	Calakmul Forest, Mexico	20.7 photos/1000 camera-days	Sánchez-Pinzón et al. (2020)
T. pecari	Mesoamerica	Occupancy rate = 0.19	Thornton et al. (2020)
T. pecari	Calakmul Forest, Mexico	Occupancy prob = 30% (rainy season), 88% (dry season)	Briceño et al. (2022)
T. pecari	Lacandon Forest, Mexico	Occupancy prob = 0.20	Falconi-Briones et al. (2022) and Falconi et al. (unpublished data)
T. pecari	Calakmul Forest, Mexico	Occupancy prob = 0.61 (2014), 0.96 (2020); detection prob = 0.09 (2014), 0.13 (2020)	Reyna-Hurtado et al. (unpublished data)
P. tajacu	Lacandon Forest, Mexico	2.3 ind/km^2; 54.3 tracks/100 km	Bolaños and Naranjo (2001)
P. tajacu	Lacandon Forest, Mexico	1.2 ind/km^2 (hunted sites), 1.5 ind/km^2 (unhunted sites)	Naranjo and Bodmer (2007)
P. tajacu	Calakmul Forest, Mexico	97 tracks/100 km (hunted sites); 86 tracks/100 km (unhunted sites)	Reyna-Hurtado and Tanner (2007)
P. tajacu	Northern Yucatan Peninsula, Mexico	1.9 ind/km^2	González-Marín et al. (2008)

(continued)

Table 7.2 (continued)

Species	Study site	Abundance/density/occupancy	Source
P. tajacu	Lacandon Forest, Mexico	80.2 tracks/100 km	Tejeda-Cruz et al. (2009)
P. tajacu	Yucatan Peninsula, Mexico	Occupancy rate = 0.91	Urquiza-Haas et al. (2009)
P. tajacu	Northern Yucatan Peninsula, Mexico	15.4 photos/1000 camera-days	Hernández-Pérez et al. (2015)
P. tajacu	Calakmul Forest. Mexico	27.5 photos/1000 camera-days and 95 tracks/100 km (unhunted sites); 3.7 photos/1000 camera-days and 56 tracks/100 km (hunted sites)	Briceño et al. (2016)
P. tajacu	Lacandon Forest, Mexico	11.9 photos/1000 camera-days; 8 tracks/100 km	Falconi (2017)
P. tajacu	Peten Forest, Guatemala	14 photos/1000 camera-days (wet season), 70.2 photos/1000 camera-days (dry season)	Moreira et al. (2019b)
P. tajacu	Lacandon Forest, Mexico	10.2 photos/1000 camera-days and 12.4 tracks/100 km (hunted sites); 20 photos/1000 camera-days and 10.3 tracks/100 km (unhunted sites)	Naranjo (2019)
P. tajacu	Calakmul Forest, Mexico	32.2 photos/1000 camera-days (water holes)	Sánchez-Pinzón et al. (2020)
P. tajacu	Mesoamerica	Occupancy rate = 0.51	Thornton et al. (2020)
P. tajacu	Lacandon Forest, Mexico	Occupancy prob = 0.60	Falconi-Briones et al. (2022) and Falconi et al. (unpublished data)
P. tajacu	Calakmul Forest, Mexico	Occupancy prob = 0.82 (2014), 1.0 (2020); detection prob = 0.6 (2014), 0.13 (2020)	Reyna-Hurtado et al. (unpublished data)

using distance sampling, while just 5 (14.7%) dealt with occupancy assessed through camera trapping. In fact, all occupancy surveys reviewed were produced between 2015 and 2022 (Tables 7.1, 7.2, and 7.3). Camera trapping was by far the most frequent method ($n = 24$; 70.6%) applied in the 34 surveys reviewed to estimate the relative abundance, density, and occupancy of ungulates in the study area. Direct sightings and track counts along line transects were used in 17 (50%) surveys, in some cases in addition to camera trapping, and just 1 (2.9%) occupancy assessment was performed using questionnaires (Tables 7.1, 7.2, and 7.3).

Table 7.3 Abundance, density, and occupancy estimates of red brocket deer (*Mazama temama*), Yucatan brown brocket deer (*Mazama pandora*), and white-tailed deer (*Odocoileus virginianus*) in the Maya Forest

Species	Study site	Abundance/density/occupancy	Source
M. temama	Lacandon Forest, Mexico	0.29 ind/km^2; 30.3 tracks/100 km	Bolaños and Naranjo (2001)
M. temama and *M. pandora*	Calakmul Forest, Mexico	100 tracks/100 km (fixed transects), 180 tracks/100 km (random transects); 3 ind/100 km (fixed transects), 2.1 ind/100 km (random transects); 0.9 ind/km^2 (fixed transects), 0.09 ind/km^2 (random transects)	Weber (2005)
M. temama	Lacandon Forest, Mexico	0.2 ind/km^2 (unhunted sites), 0.33 ind/km^2 (hunted sites)	Naranjo and Bodmer (2007)
M. temama and *M. pandora*	Calakmul Forest, Mexico	674 tracks/100 km (hunted sites), 636 tracks/100 km (unhunted sites)	Reyna-Hurtado and Tanner (2007)
M. temama	Lacandon Forest, Mexico	167.7 tracks/100 km	Tejeda-Cruz et al. (2009)
M. temama	Yucatan Peninsula, Mexico	Occupancy rate = 0.84	Urquiza-Haas et al. (2009)
M. temama	Calakmul Forest, Mexico	28.8 photos/1000 camera-days	Moreira et al. (2019a)
M. temama	Peten Forest, Guatemala	12.5 photos/1000 camera-days	Moreira et al. (2019a)
M. pandora	Calakmul Forest, Mexico	3.0 photos/1000 camera-days (hunted site), 3.6 photos/1000 camera-days (unhunted site)	Moreira et al. (2019a)
M. temama		8.5 photos/1000 camera-days and 8.1 tracks/100 km (hunted sites), 9.7 photos/1000 camera-days and 16.3 tracks/100 km (unhunted sites)	Naranjo (2019)
M. pandora	Calakmul Forest, Mexico	Occupancy prob = 0.42 (2014), 0.7 (2020); detection prob = 0.03 (2014), 0.14 (2020)	Reyna-Hurtado et al. (unpublished data)
M. temama	Lacandon Forest, Mexico	Occupancy prob = 0.35	Falconi et al. (unpublished data)
O. virginianus	Lacandon Forest, Mexico	0.5 tracks/100 km	Bolaños and Naranjo (2001)
O. virginianus	Calakmul Forest, Mexico	0.9 tracks/100 km (fixed transects), 1.8 tracks/100 km (random transects); 1 ind/100 km (fixed transects), 0.8 ind/100 km (random transects); 0.02 ind/km^2 (fixed transects), 0.009 ind/km^2 (random transects)	Weber (2005)
O. virginianus	Calakmul Forest, Mexico	88 tracks/100 km (hunted sites), 24 tracks/100 km (unhunted sites)	Reyna-Hurtado and Tanner (2007)

(continued)

Table 7.3 (continued)

Species	Study site	Abundance/density/occupancy	Source
O. virginianus	Northern Yucatan Peninsula, Mexico	5.5 ind/km^2; 13 ind/100 km	González-Marín et al. (2008)
O. virginianus	Lacandon Forest, Mexico	0.04 ind/km^2 (unhunted sites), 0.29 ind/km^2 (hunted sites)	Naranjo (2008)
O. virginianus	Lacandon Forest, Mexico	24.6 tracks/100 km	Tejeda-Cruz et al. (2009)
O. virginianus	Yucatan Peninsula, Mexico	Occupancy rate = 0.92	Urquiza-Haas et al. (2009)
O. virginianus	Northern Yucatan Peninsula, Mexico	21.3 photos/1000 camera-days	Hernández-Pérez et al. (2015)
O. virginianus	Peten Forest, Guatemala	48.9 photos/1000 camera-days	Moreira et al. (2019a)
O. virginianus	Lacandon Forest, Mexico	1.7 photos/1000 camera-days, 0.8 ind/100 km, and 12.4 tracks/100 km (hunted sites); 0.7 photos/1000 camera-days, 0.3 ind/100 km, and 0.9 tracks/100 km (unhunted sites)	Naranjo (2019)
O. virginianus	Calakmul Forest, Mexico	Occupancy prob = 0.75 (2014), 1.0 (2020); detection prob = 0.15 (2014), 0.22 (2020)	Reyna-Hurtado et al. (unpublished data)

7.3.1 Abundance and Density

7.3.1.1 Baird's Tapir

Baird's tapir has been the third most studied ungulate in the Maya Forest after the white-lipped peccary and the collared peccary (Table 7.1). Its relative abundance has been estimated through visual encounters in transect samplings, track counts, and photo trapping in several sites for the last 20 years. Naranjo (2018) provided an overview of tapir abundance across southern Mexico, noting that previous studies have allowed estimating 0.03–0.45 tapirs/100 km traveled, and 3.8–37.6 tapir photographs/1000 camera-days. Waterholes in Calakmul, the Lacantun River basin in the Lacandon Forest, and the subdeciduous tropical forest in Balam-Kin Reserve were the sites with the highest abundance indices (Pérez-Cortez et al. 2012; Carrillo-Reyna et al. 2015; Naranjo et al. 2015).

In the Lacandon Forest, Bolaños and Naranjo (2001) and later Tejeda-Cruz et al. (2009) observed 26.1 and 57.7 Baird's tapir tracks per 100 km traveled, respectively. In the same region, Falconi (2017) estimated abundance indices of 10.8 photographs/1000 camera-days, 0.76 tapirs sighted/100 km traveled, and 10.3 tracks/100 km traveled. In the waterholes of Calakmul, Pérez-Cortez (2011) recorded an average of 37.6 photographs/1000 camera-days for 3 years, and 148 tracks/100 km

Fig. 7.4 Baird's tapir (*Tapirus bairdii*) in Montes Azules Biosphere Reserve, Lacandon Forest, Chiapas, Mexico. (Photograph by Eduardo J. Naranjo)

traveled. In more extensive samplings of Calakmul, Reyna-Hurtado and Tanner (2007) observed 42 and 3 tracks/100 km in hunted and unhunted sites, respectively, while Carrillo-Reyna et al. (2015) registered 17 photographs/1000 camera-days and 33 tracks/100 km. The only density estimates for Baird's tapir in the Maya Forest were done by Bolaños and Naranjo (2001) and by Naranjo and Bodmer (2007), ranging from 0.05 to 0.24 tapirs/km^2 in hunted and unhunted sites of the Lacandon Forest, respectively (Fig. 7.4).

It is worth mentioning that Baird's tapir densities have also been estimated in other regions of southeast Mexico, outside of the Maya Forest. In the Sierra Madre de Chiapas, Lira et al. (2004) assessed a density of 0.07 tapirs/km^2 through distance sampling at El Triunfo Biosphere Reserve, while Carbajal-Borges et al. (2014) and later Rivero et al. (2022) used camera trapping and hierarchical modeling to calculate densities of 0.12 and 0.1 ind/km^2, respectively.

7.3.1.2 White-Lipped Peccary

The white-lipped peccary has been the most frequently studied ungulate species in the Greater Maya Forest. Its abundance and density have been analyzed mainly in Calakmul, the Lacandon Forest (Fig. 7.5), and the Peten Forest, Guatemala (Novack et al. 2005; Reyna-Hurtado et al. 2019; Table 7.2). Naranjo et al. (2015) recorded abundances of 1.7–13.3 photographs/1000 camera-days, and 1.5–6.3 tracks/100 km traveled in several sites of the Maya Forest (Lacandon Forest, Calakmul, Balam-Kin, Ejido Caobas, and Sian Ka'an). In the Lacandon Forest, Bolaños and Naranjo (2001) and Tejeda-Cruz et al. (2009) detected 9.4 and 2.2 tracks/100 km traveled,

Fig. 7.5 White-lipped peccaries (*Tayassu pecari*) in Montes Azules Biosphere Reserve, Lacandon Forest, Chiapas, Mexico. (Photograph by Eduardo J. Naranjo)

respectively, while Falconi (2017) reported 80.9 photographs/1000 camera-days, 18.9 peccaries sighted/100 km traveled, and 7.6 tracks/100 km. Sánchez-Pinzón et al. (2020) recorded 20.7 photographs/1000 camera-days in a 5-year study of several Calakmul waterholes. In the same region, Reyna-Hurtado and Tanner (2007) compared the abundance of white-lipped peccaries in hunted and unhunted sites, recording 8 versus 24 tracks/100 km. Similarly, Briceño et al. (2016) obtained 10 versus 18.4 photographs/1000 camera-days, and 11 versus 16 tracks/100 km in hunted and unhunted sites, respectively.

Using radiotelemetry and analyzing the home range areas of four groups, Reyna-Hurtado et al. (2010) estimated a density of 0.43 white-lipped peccaries/km^2 in Calakmul Biosphere Reserve. On their side, Bolaños and Naranjo (2001) detected 3.8 peccaries/km^2, while Naranjo and Bodmer (2007) registered 1.1 and 7.9 ind/km^2 in slightly hunted and persistently hunted sites of the Lacandon Forest, respectively. In northern Guatemala, Novack et al. (2005) found a density of 9.6 peccaries/km^2 in an unhunted site of the Peten Forest.

7.3.1.3 Collared Peccary

In sites with different hunting pressure in the Calakmul region, Reyna-Hurtado and Tanner (2007) detected 97 (hunted sites) versus 86 (unhunted sites) tracks/100 km. A decade later, Briceño et al. (2016) estimated an abundance of 27.5 collared-peccary photographs/1000 camera-days and 95 tracks/100 km (unhunted site), versus 3.7 photographs/1000 camera-days and 56 tracks/100 km (hunted site). In waterholes across the same region, Sánchez-Pinzón et al. (2020) recorded 32.2 photographs/1000 camera-days. The only assessment of collared peccaries' abundance in the northern Yucatan Peninsula was done by Hernández-Pérez et al. (2015), who detected 15.4 photographs/1000 camera-days in Los Petenes, Dzilam, and El Palmar preserves. In the Lacandon Forest, Bolaños and Naranjo (2001) and Tejeda-Cruz et al. (2009) recorded 54.3 and 80.2 tracks/100 km traveled, respectively. Later, Falconi (2017) obtained 11.9 photographs/1000 camera-days, and 8 tracks/100 km traveled, while Naranjo (2019) found 10.2 versus 20 photographs/1000 camera-days, and 12.4 versus 10.3 tracks/100 km in hunted and unhunted sites, respectively.

The density of collared peccaries has been studied relatively little in the Maya Forest (Table 7.2). It was first estimated by Bolaños and Naranjo (2001) at 2.3 peccaries/km^2 in pristine sites within Montes Azules Biosphere Reserve in the Lacandon Forest. In a more comprehensive study, Naranjo and Bodmer (2007) recorded 1.2 and 1.5 peccaries/km^2 in persistently hunted and slightly hunted sites of the Lacandon Forest, respectively. Finally, González-Marín et al. (2008) observed a density of 1.9 peccaries/km^2 in the tropical dry forest of the northern Yucatan Peninsula (El Edén reserve).

7.3.1.4 Red Brocket Deer and Yucatan Brown Brocket Deer

The abundances and densities of the red brocket and the Yucatan brown brocket deer (Fig. 7.6) have been considerably less studied than those of peccaries and tapirs in the Maya Forest (Table 7.3). In the Calakmul region, Weber (2005) estimated an

Fig. 7.6 Yucatan brown brocket deer (*Mazama pandora*) in the Balamkú Reserve, Calakmul Forest, Campeche, Mexico. (Photograph by Eduardo J. Naranjo)

overall abundance of *Mazama temama* and *M. pandora* between 100 and 180 tracks/100 km, and between 3 and 2.1 sightings/100 km, depending on the sampling technique used (either fixed permanent transects or stratified random transects). On their side, Reyna-Hurtado and Tanner (2007) estimated much higher abundances of 674 (hunted sites) versus 636 (unhunted sites) brocket deer tracks/100 km, and they found that brocket deer were the most common ungulates in the Calakmul Biosphere Reserve and three surrounding communities. Using camera trapping, Moreira et al. (2019a) obtained 28.8 red brocket deer photographs/1000 camera-days in Ejido Nuevo Becal. The same authors detected 3.0 and 3.6 Yucatan brown brocket deer photographs/1000 camera-days in Ejido Nuevo Becal (hunted site) and Calakmul Biosphere Reserve (unhunted site), respectively.

In the Lacandon Forest, Bolaños and Naranjo (2001) and Tejeda-Cruz et al. (2009) detected 30.3 and 167.7 tracks/100 km traveled, respectively. In different localities of the Lacandon Forest, Naranjo (2019) reported 8.5 versus 9.7 red brocket deer photographs/1000 camera-days, and 8.1 versus 16.3 tracks/100 km in persistently hunted sites and slightly hunted sites, respectively. In Laguna del Tigre National Park, Guatemala, Moreira et al. (2019a) registered 12.5 red brocket deer photographs/1000 camera-days. The density of *Mazama* spp. was estimated by Weber (2005) at 0.9 (fixed transects) and 0.09 (random transects) deer/km^2 in the Calakmul region. In the Lacandon Forest, Bolaños and Naranjo (2001) detected a density of 0.29 deer/km^2, while Naranjo and Bodmer (2007) estimated 0.2 and 0.33 ind/km^2 in slightly hunted and persistently hunted sites, respectively.

7.3.1.5 White-Tailed Deer

Weber (2005) estimated white-tailed deer abundances in the Calakmul region, recording direct sightings and tracks through two transect-sampling techniques: fixed permanent transects and stratified temporary random transects. He registered 1.0 (fixed transects) and 0.8 (random transects) deer sighted/100 km, as well as 0.9 (fixed) and 1.8 (random) tracks/100 km. In another study in Calakmul, Reyna-Hurtado and Tanner (2007) observed considerably higher abundances of 88 (hunted sites) versus 24 (unhunted sites) tracks/100 km. In the northern Yucatan Peninsula, González-Marín et al. (2008) sighted 13 deer/100 km in El Eden Reserve, while Hernández-Pérez et al. (2015) obtained 21.3 photographs/1000 camera-days in Los Petenes, Dzilam, and El Palmar. In the Lacandon Forest, Bolaños and Naranjo (2001) and Tejeda-Cruz et al. (2009) observed 0.5 and 24.6 tracks/100 km traveled, respectively. Later, Naranjo (2019) registered 0.3 (slightly hunted) versus 0.8 (persistently hunted) sightings/100 km, 0.9 versus 12.4 tracks/100 km, and 0.7 versus 1.7 photographs/100 km in the same region. The only published study available on the abundance of white-tailed deer in the Guatemalan portion of the Maya Forest was done by Moreira et al. (2019a). They estimated an abundance of 48.9 photographs/1000 camera-days in Laguna del Tigre National Park. The density of this ungulate was estimated by Weber (2005) at 0.02 (fixed transects) and 0.009 (random transects) deer/km^2 in the Calakmul region, by González-Marín et al.

(2008) at 5.5 deer/km^2, in El Eden Reserve, and by Naranjo (2008) at 0.04 and 0.29 deer/km^2 in slightly hunted and persistently hunted sites of the Lacandon Forest, respectively.

7.3.2 Occupancy

Habitat use of ungulate species has been a frequent research topic in the Maya Forest for at least two decades (e.g., Reyna-Hurtado and Tanner 2005; Tejeda-Cruz et al. 2009; Gallina-Tessaro et al. 2019; Mandujano and Reyna-Hurtado 2019; Naranjo 2019). However, habitat occupancy of ungulates using hierarchical models has just started to be addressed in recent years in southeast Mexico. The first study was conducted by De la Torre et al. (2018) who estimated an occupancy probability of 0.02 for Baird's tapirs in the Sierra Madre de Chiapas. In the Maya Forest, Martínez et al. (2021) conducted a comprehensive study of Baird's tapir occupancy in the Runaway Creek Nature Reserve (RCNR), Belize, with a sampling effort of 8932 camera-trap days between 2015 and 2019. These authors estimated a cumulative naïve occupancy of 85.7%, a probability of occupancy of 0.97, and a detection probability of 0.14 (Table 7.1). The habitat variables with the strongest effect on tapir occupancy were distance to roads ($\beta = -0.95$, AIC $= 0.14$) and distance to human settlements ($\beta = 0.77$, AIC $= 0.11$). In a similar study in the Lacandon Forest, Falconi-Briones et al. (2022) and Falconi et al. (unpublished data) found that the variables that best explain the occupancy of tapirs are distance to permanent water bodies, distance to roads, and presence of evergreen tropical forest and secondary tropical forest (Occupancy probability = 0.50; Table 7.1). In particular, the probability of tapir occupancy increases as the distance to water bodies decreases in their study area.

Four studies have analyzed the occupancy of peccaries in the Maya Forest. The first was conducted by Falconi-Briones et al. (2022) and later complemented by Falconi et al. (unpublished data). They observed that white-lipped peccaries showed a higher occupancy probability (Occupancy probability = 0.20) in sites with less human disturbance, far from villages and roads, and closer to permanent water bodies. On the contrary, collared peccaries had a higher occupancy probability (0.60) far from water bodies and nearby roads and human settlements. The second study was done by Briceño et al. (2022) in Calakmul, where the occupancy probability in the rainy and the dry seasons was 0.30 versus 0.88 for the white-lipped peccary and 0.40 versus 0.44 for the collared peccary. These authors detected that the occupancy of both peccary species was primarily affected by water availability, hunting, habitat type, and predator presence in Ejido Nuevo Becal, nearby the Calakmul Biosphere Reserve.

The third study was conducted by Urquiza-Haas et al. (2009) using an alternative method based on interviews with local hunters at 147 forest patches in the eastern Yucatan Peninsula. The proportions of forest patch occupancy were estimated for game species, including the white-lipped peccary (present in 4% of patches), collared peccary (91.2%), Baird's tapir (12.2%), brocket deer (84.4%), and white-tailed deer (91.8%). Human density, hunting, and the quality of forest cover were the most significant predictors of species' occupancy (Urquiza-Haas et al. 2009). The fourth study of peccary occupancy was not conducted just for the Maya Forest but included all populations in Mesoamerica (Thornton et al. 2020). The best occupancy model found by these authors for white-lipped and collared peccaries included human influence (0.26, 0.16) and elevation (0.50, 0.40) as the most significant variables analyzed. Occupancy of both species was negatively affected by the human footprint (measured through an array of variables). Nonetheless, the white-lipped peccary showed more vulnerability than the collared peccary. The occupancy rates estimated across Mesoamerica in this study were 0.19 and 0.51 for white-lipped and collared peccaries, respectively (Thornton et al. 2020).

Recently, R. Reyna-Hurtado et al. (unpublished data) estimated the occupancy rate and detection probability of five ungulate species present in waterholes between 2014 and 2020 in the Calakmul Biosphere Reserve. They estimated tapir occupancy at 0.73 (2014) versus 0.826 (2020), and the detection probabilities were 0.10 (2014) versus 0.262 (2020). White-lipped peccary occupancy varied from 0.61 to 0.96, and its detection probabilities were 0.09–0.134 in 2014 and 2020, respectively. Similarly, collared peccary occupancy was 0.82 and 1.0, with detection probabilities of 0.06 and 0.13. White-tailed deer occupancy was 0.75 and 1.0, with detection probabilities of 0.15 and 0.22. Finally, Yucatan brown brocket deer occupancy was 0.42 and 0.70, while its detection probabilities were 0.03 and 0.14 (Reyna-Hurtado et al., unpublished data). Finally, Falconi et al. (unpublished data) conducted the first assessment of the occupancy probability (0.35) of the red brocket deer in the Lacandon Forest using a hierarchical approach.

7.4 Information Gaps and Needs

A growing number of studies on the abundance and density of ungulate species have been done in the Maya Forest, especially during the last decade. However, most of these studies have focused on evaluating population abundance through track counts, visual encounters, and especially camera trapping during the last 15 years. In contrast, density estimations and occupancy have rarely been included in those surveys. For many researchers interested in Neotropical mammals, large predators and primates are far more attractive than ungulates as subjects of study. In addition, more international funding for research is available for the first. Consequently, most surveys on large- and medium-sized species of the Maya Forest have been focused on carnivores and primates. In comparison, ungulates have received much less attention.

The density and occupancy of felines (i.e., jaguar, puma, and ocelot) have been assessed for the last two decades in several localities of the Maya Forest (see this volume). Nonetheless, few studies evaluating those variables have been conducted on ungulates as focal species. Within this group, peccaries and tapirs have been the

Fig. 7.7 View of the tropical forest around the ancient Maya city of Calakmul inside Calakmul Biosphere Reserve, Campeche, Mexico. (Photograph by Eduardo J. Naranjo)

most frequent objects of study in this region, while the white-tailed deer and brocket deer (both red and brown) have received less attention. This difference can be understandable considering that deer are not as endangered and are less charismatic to the public compared to tapirs and white-lipped peccaries.

Geographically speaking, the assessments of relative abundance, density, and occupancy of ungulates in the Maya Forest have been concentrated within and nearby the largest protected areas of the region: Calakmul (Fig. 7.7), Montes Azules, and Sian Ka’an Biosphere Reserves in Mexico, the Maya Biosphere Reserve, Tikal, and Laguna del Tigre National Parks in Guatemala, and the Runaway Creek Nature Reserve in Belize. Good habitat quality, extensive forest cover, and expected higher population densities help explain why most of the surveys have been focused on sites within protected areas compared to fragmented community lands far away from the main roads. In some cases, infrastructure (e.g., lodging and facilities) may bias the location of the sampling sites. In others, accessibility and security issues have severely limited research outside protected areas.

In terms of methodologies, it is evident that since digital photography became widely available after 2005, camera trapping has become by far the most popular technique to assess the relative abundance, density, and occupancy of medium- and large-sized forest mammals worldwide, especially within the last decade. An unwanted effect of this trend is that formerly standard methods that could be complementary to camera trapping such as distance sampling, track counts, feces counts, and radiotelemetry have been underestimated and less used by young researchers.

In summary, more information on the relative abundance, density, and occupancy of the native ungulate species is needed outside the largest protected areas in the Maya Forest. Further studies should explore the factors driving ungulate occupancy-abundance relationships, including habitat connectivity conditions at larger scales in the region. It is also important to continue developing long-term studies on these variables for Baird's tapir and the white-lipped peccary in the region as long as they are endangered. We suggest encouraging this kind of research wherever deer, peccary, and tapir populations are present in community lands (i.e., indigenous territories, ejidos) and large properties not necessarily contiguous to the biosphere reserves and national parks in Belize, northern Guatemala, and southeast Mexico.

7.5 Implications for Conservation

The information available on the abundance, density, and occupancy of ungulates may be useful to support conservation decisions, particularly in areas of the Maya Forest where there has been ongoing research for about two decades. For instance, Naranjo (2019) compared shifts in the abundances of the five ungulates (Baird's tapir, white-lipped peccary, collared peccary, white-tailed deer, and red brocket deer) present in the Lacandon Forest, Mexico, between 2001 and 2011. He found that overall abundances differed among species and sampling techniques used.

In his survey, Naranjo (2019) detected considerably higher abundances (from direct sightings and camera trapping) of Baird's tapirs and white-lipped peccaries in pristine sites within Montes Azules Biosphere Reserve (MABR; Fig. 7.8) than in surrounding community lands, where subsistence hunting is a common practice. Nonetheless, the abundances of collared peccaries, white-tailed deer, and red brocket deer were similar between the two areas. Interestingly, the abundance of Baird's tapir declined (−59.7%) between 2001 and 2011, while the white-tailed deer jumped by 421%. The other ungulates increased their abundances by 64% (white-lipped peccary), 37% (collared peccary), and 22% (red brocket deer) within the same period. These shifts may be due to forest fragmentation associated with human population growth, changes in farming and hunting practices, and growing environmental awareness among residents (Naranjo et al. 2015; Naranjo 2018).

In another long-term study, Reyna-Hurtado et al. (2019) found that tapir occupancy probabilities remained stable during 11 years of monitoring waterholes across the Calakmul Biosphere Reserve despite large variations in water availability. Contrastingly, white-lipped peccary populations showed dramatic changes in their occupancy probabilities as they disappeared from several sites of the Reserve in the driest years (2017, 2018, 2019; Reyna-Hurtado et al. unpublished data).

These results shed light on the need for controlling the primary threats for endangered tapirs and white-lipped peccary populations in both the Lacandon Forest

Fig. 7.8 View of Laguna Miramar within Montes Azules Biosphere Reserve, Lacandon Forest, Chiapas, Mexico. (Photograph by Eduardo J. Naranjo)

and the Calakmul Forest: poaching and habitat fragmentation around the protected areas. The human population and land use change for farming and cattle ranching are rapidly expanding in these regions and the Greater Maya Forest. Therefore, a major impact on native ungulate populations is expected in the long term. While this impact would be negative for tapirs and white-lipped peccaries, it might not severely harm the other species present. Although the red brocket deer, the Yucatan brown brocket deer, the white-tailed deer, and the collared peccary are relatively tolerant to habitat disturbance and moderate hunting, measures to mitigate deforestation and poaching at the community level would also benefit them across the region.

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Part II
Case Studies

Chapter 8
Factors Influencing Habitat Occupancy by the Spotted Paca (*Cuniculus paca*) in Oaxaca, Mexico

Erika García-Casimiro and Antonio Santos-Moreno

Abstract The spotted paca (*Cuniculus paca*), one of the largest rodent species in the Neotropics, is a seed disperser of plants with large fruits and important prey for large predators and human communities, but it is subject to heavy hunting pressure in large parts of its range. This study aimed to identify the main factors affecting the occurrence of paca in a tropical subdeciduous forest in the Sierra Norte de Oaxaca, southeastern Mexico, using occupancy models and eight environmental covariables. We obtained 202 independent records from 20 camera traps to model the occupancy and detectability of the paca in the rainy season of 2017 and in the dry season of 2018. In the rainy season, the occupancy probability was 0.841, and the probability of detection was low (0.266) and showed an inverse relationship with distance to water bodies. There was no clear relationship among the covariates that described the paca habitat and its occupancy probability; however, in the dry season, the occupancy probability was negatively related to distance to water bodies and positively related to predation cover. The paca detection probability also showed a negative relationship with distance to water bodies. Our results suggest that there are still gaps in our knowledge about factors driving habitat occupancy by pacas in Mexico. We consider it necessary to assess additional habitat characteristics such as the presence of predators and competitors to model the occupancy dynamics of this species more accurately.

Keywords Camera trapping · Detectability · Habitat use · Occupancy modeling

8.1 Introduction

As natural habitat fragmentation and loss continue to increase worldwide; many mammal populations have suffered dramatic reductions in their populations, making it imperative to have the necessary information to ensure proper management (Long

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Fig. 8.1 Spotted paca (*Cuniculus paca*) registered with a camera trap in San Martín Soyolapam, Santiago Comaltepec, Oaxaca, Mexico (Photograph by Antonio Santos-Moreno)

and Zielinski 2008). However, inferences about habitat requirements of mammals are scarce due to the problems involved in conducting rigorous studies at the required spatial and temporal scales (Karanth et al. 2006). The spotted paca (*Cuniculus paca*) has reduced its population size considerably due to habitat loss and hunting pressure throughout the Neotropics (Urquiza-Haas et al. 2009; Emmons 2016) (Fig. 8.1). Although it is currently in the category of Least Concern by the IUCN (Emmons 2016), local extinctions have been reported in the southeast of its range. This species is important for ecosystems and human communities; fulfills ecological roles as seed disperser and predator (Camargo-Sanabria and Mendoza 2016; De Osma et al. 2014; Beck-King et al. 1999), contributing to microclimate regulation and nutrient recycling, among other processes (De Osma et al. 2014; Cartaya et al. 2016). Therefore, its absence influences the regeneration of plant species (Terborgh and Wright 1994; Galetti et al. 2006; Jorge and Howe 2009). In many areas of South America, large seed dispersers such as peccaries and tapirs have suffered drastic reductions in the size of their populations, and even local extirpation, so the only native species capable of dispersing these fruits and seeds is the paca (Nagy-Reis et al. 2019).

Pacas are important in the diet of medium- and large-sized carnivorous mammals (Emmons 1987; Pérez 1992; Blake et al. 2012); likewise, the meat of this rodent is consumed in many communities throughout its range (Altrichter 1999; Smythe 1987). For these reasons, it is necessary to ensure the sustainable management of this species. However, without accurate estimates about its ecological parameters and the characteristics of its habitat, it is difficult to determine with certainty whether its populations and their habitat are in good condition, so it is important to assess those features to design conservation and use strategies ensuring the long-term conservation of this mammal (Moreno-Valdez et al. 1997; Aquino et al. 2009; Parroquin et al. 2010).

Although habitat use is the subject of many studies of mammals, studies concerning factors that may influence paca occupancy are limited (Figueroa de León et al. 2016; Ferreguetti et al. 2018). Occupancy modeling has become a popular tool for investigating species occurrence over temporal and spatial scales (Mackenzie et al. 2002); these models explore simultaneously habitat and anthropogenic variables that influence species distribution and provide robust inference for species difficult to observe under natural conditions (MacKenzie et al. 2017). Given the importance of establishing the factors that influence habitat use by pacas in heterogeneous landscapes, the purpose of this study was to estimate the variables influencing paca occupancy in a tropical subdeciduous forest of the Sierra Norte, Oaxaca, Mexico.

8.2 Methods

8.2.1 Study Area

The study was conducted in the community of San Martín Soyolapam, municipality of Santiago Comaltepec in the Sierra Norte region of the state of Oaxaca, Mexico (Fig. 8.2). The altitude ranges from 100 to 800 m. The climate is tropical seasonal, with an average annual temperature from 10 to 26 °C and average annual rainfall from 800 to 400 mm (INEGI 2005). The rainy season runs from June to December and the dry season from January to May. The vegetation is mainly tropical subdeciduous forest, with a 20–30 m canopy composed by species such as *Manilkara chicle*, *Protium copal*, *Tabebuia rosea*, *Cedrela odorata*, *Albizia guachapele*, *Brosimum alicastrum*, *Aspidosperma megalocarpon*, and S*chizolobium parahandba*. This forest has a medium arboreal stratum (10–15 m) with presence of *Cupania dentata*, *Heliocarpus appendiculatus*, *Pseudobombax ellipticum*, *Cordia alliodora*, *Lonchocarpus lineatus*, *Acosmium panamense*, *Castilla elastica*, and *Vochysia guatemalensis*. There is a lower tree stratum (4–8 m) with *Tabernaemontana alba*, *Crataeva tapia*, *Pleuranthodendron linaenii*, *Exostema mexicanum*, *Astronium graveolens*, *Louteridium donnell-smithii*, *Pouteria durlandii*, *Faramea occidentalis*, *Lonchocarpus guatemalensis*, *Ficus maxima*, *Stemmadenia donnell-smithii*, and *Rechia mexicana*. In the understory, there is presence of *Rinorea hummelii*, *Chamaedorea elatior*, *Ch. tepejilote*, *Anthuria schlechtendalii*, several fern species, and vines such as *Desmoncus chinantlensis*, *Dioscorea mandxicana*, *Philodandndron* spp., and *Syngonium* spp. Agricultural areas, pastures, and human settlements alternate with the natural vegetation (Torres-Colín 2004).

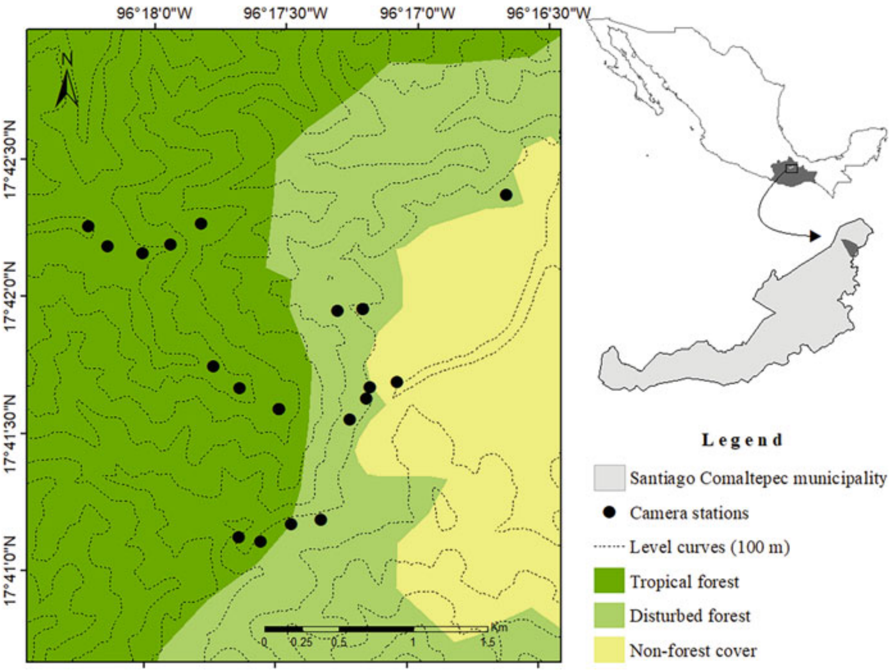

Fig. 8.2 Location of the study area in the Sierra Norte of Oaxaca, México. Black dots represent the sites where the camera traps were placed

8.2.2 Data Collection

From June 2016 to June 2018, sampling was carried out using photo traps in the study area. Twenty sampling stations were placed on trails, mountain edges, ravines, dry streams, and riverbanks, spaced at distances between 0.2 and 1.5 km apart, depending on terrain conditions. This distance was selected considering that the average home range of the paca is 2 ha (Beck-King et al. 1999). At each sampling station, a Bushnell Trophy Cam™ model camera trap with a passive infrared sensor was placed at a height of no more than 40 cm above ground level, according to the topography and inclination of the sampling area. The cameras were programmed to remain active for 24 h, taking three photos and one video from 10 to 20 s per event, with an interval of 1 s between the last photo and the video. Each trap was placed at least two meters away from the closest point where it was considered that an animal could cross the detection field of the sensor. All obstacles such as plants and branches were removed from the area near the camera since any obstruction to the sensor decreases the detection capacity of the camera trap and can produce inadequate photographs. The position of each camera was georeferenced with a Garmin e-Trex 20× model GPS. Cameras tramps collected data in the field continuously for

2 years and were checked once a month, to obtain general data between visits and to replace dead batteries, memory cards, and misfunctioning cameras.

8.2.3 Habitat Covariates

In each season, the characteristics of the vegetation of each photo-trapping station were recorded (Fig. 8.3). Nine habitat covariates that could potentially influence the probabilities of paca occupancy and detection were measured (Table 8.1). Three spatial variables were measured; the abbreviations used to identify them in Tables 8.1 and 8.2 are shown in parentheses: distance to water bodies (Water); distance to roads (Roads); and distance to towns (Towns). These variables were calculated using the geoprocessing tools available in ArcGis (ESRI 2010).

Six habitat structure variables were measured (Table 8.1). At each sampling station, rectangular plots of 400 m^2 were established and centered at the point where each photo trap was placed. In each plot, the tree density (TreeDensity) was obtained, that is, the number of trees per unit area (Higgins et al. 1996), and all trees with a diameter at breast height (DBH) $\geq$ 10 cm were counted. Each tree was measured with a dimetric tape at a height of 1.3 m from the ground surface. Tree height (TreeHeight) was measured with a clinometer at a fixed distance of 15 m to the base of the tree. Measurements of canopy coverage (CanopyCoverage) were made by looking at the four cardinal points with a concave spherical densitometer at each sampling station. Vertical protection coverage (VPC) was measured by looking

Fig. 8.3 View of the habitat of the spotted paca in San Martín Soyolapam, Santiago Comaltepec, Oaxaca, Mexico (Photograph by Antonio Santos-Moreno)

Table 8.1 Pearson correlation matrix among habitat covariates of the 2017 rainy season (below the main diagonal) and 2018 dry season (above the main diagonal); significance is shown in parentheses

	Water	Roads	Towns	VPC[a]	Slope	CanopyCoverage	TreeDensity	DBH[b]	TreeHeight
Water	**2.33, 2.28**	−0.58 (0.01)	0.28 (0.28)	−0.15 (0.55)	−0.18 (0.49)	0.29 (0.25)	−0.02 (0.93)	0.01 (0.96)	0.25 (0.34)
Roads	−0.58 (0.01)	**2.07, 2.2**	−0.27 (0.30)	−0.11 (0.66)	0.22 (0.40)	0.1 (0.70)	−0.12 (0.65)	0.06 (0.83)	0.2 (0.45)
Towns	0.31 (0.20)	−0.21 (0.38)	**1.79, 2.57**	0.1 (0.70)	0 (0.99)	0.49 (0.05)	0.1 (0.70)	−0.22 (0.40)	0.03 (0.92)
VPC[a]	−0.05 (0.83)	−0.11 (0.64)	0.22 (0.38)	**2.57, 2.46**	0.1 (0.70)	−0.41 (0.10)	−0.4 (0.11)	0.38 (0.13)	−0.03 (0.92)
Slope	−0.15 (0.55)	0.18 (0.47)	−0.01 (0.97)	0.11 (0.66)	**1.33, 1.46**	−0.13 (0.63)	−0.25 (0.34)	−0.03 (0.92)	0.23 (0.38)
CanopyCoverage	0.15 (0.55)	0.11 (0.66)	0.25 (0.30)	−0.51 (0.03)	−0.13 (0.59)	**3.15, 3.9**	0.04 (0.89)	0 (0.99)	0.51 (0.04)
TreeDensity	−0.16 (0.52)	−0.07 (0.78)	−0.13 (0.59)	−0.53 (0.02)	−0.22 (0.37)	0.31 (0.20)	**2.18, 1.72**	−0.51 (0.04)	−0.38 (0.13)
DBH[b]	0.06 (0.80)	0.06 (0.82)	−0.11 (0.66)	0.43 (0.06)	−0.02 (0.93)	−0.11 (0.64)	−0.54 (0.02)	**2.11, 2.01**	0.44 (0.08)
TreeHeight	0.2 (0.42)	0.22 (0.37)	0 (0.99)	−0.07 (0.78)	0.2 (0.41)	0.5 (0.03)	−0.22 (0.36)	0.4 (0.09)	**2.73, 2.81**

The main diagonal (in bold) shows the values of the Variance Inflation Factor (VIF): the first value is from the 2017 rainy season, and the second from the 2018 dry season

[a] *VPC* vertical protection coverage

[b] *DBH* diameter at breast height

Table 8.2 Best models of *Cuniculus paca* occupancy and detection in the Sierra Norte de Oaxaca, Mexico (2017–2018)

Season and year	Model	AIC[a]	ΔAIC	AICwt[b]
Rainy season 2017	$\Psi_{(\text{CanopyCover})}, \rho_{(\text{Water})}$	237.04	0.00	0.1812
	$\Psi_{(.)}, \rho_{(\text{Water})}$	237.62	0.58	0.1355
	$\Psi_{(\text{CanopyCover + Water})}, \rho_{(\text{Water})}$	238.05	1.01	0.1095
	$\Psi_{(\text{VPC})}, \rho_{(\text{Water})}$	238.53	1.49	0.0859
	$\Psi_{(\text{Water})}, \rho_{(\text{Water})}$	238.88	1.84	0.0721
	$\Psi_{(\text{CanopyCover + VPC})}, \rho_{(\text{Water})}$	238.99	1.95	0.0685
	$\Psi(_{\text{Towns})}, \rho_{(\text{Water})}$	239.42	2.38	0.0550
	$\Psi_{(\text{TreeDensity})}, \rho_{(\text{Water})}$	239.55	2.51	0.0518
	$\Psi_{(\text{TreeHeight})}, \rho_{(\text{Water})}$	239.55	2.51	0.0516
	$\Psi_{(\text{Roads})}, \rho_{(\text{Water})}$	239.58	2.54	0.0509
	$\Psi_{(\text{DBH})}, \rho_{(\text{Water})}$	239.62	2.58	0.0499
	$\Psi_{(\text{Water + VPC})}, \rho_{(\text{Water})}$	239.89	2.85	0.0436
	$\Psi_{(\text{CanopyCover + Water + VPC})}, \rho_{(\text{Water})}$	239.92	2.88	0.0428
	$\Psi_{(.)}, \rho_{(.)}$	246.15	9.11	<0.01
Dry season 2018	$\Psi_{(\text{Water + CanopyCover + VPC})}, \rho_{(\text{Water})}$	182.29	0.00	0.780
	$\Psi_{(\text{Water + CanopyCover})}, \rho_{(\text{Water})}$	185.91	3.62	0.130
	$\Psi_{(\text{Water})}, \rho_{(\text{Water})}$	188.58	6.29	0.034
	$\Psi_{(\text{Water + Slope})}, \rho_{(\text{Water})}$	189.93	7.65	0.017
	$\Psi_{(\text{Water + VPC})}, \rho_{(\text{Water})}$	190.11	7.82	0.016
	$\Psi_{(\text{DBH})}, \rho_{(\text{Water})}$	190.81	8.52	0.011
	$\Psi_{(.)}, \rho_{(\text{Water})}$	193.39	11.10	<0.01
	$\Psi_{(\text{Roads})}, \rho_{(\text{Water})}$	194.36	12.07	<0.01
	$\Psi_{(\text{CanopyCover})}, \rho_{(\text{Water})}$	194.68	12.39	<0.01
	$\Psi_{(\text{TreeDensity})}, \rho_{(\text{Water})}$	195.17	12.88	<0.01
	$\Psi_{(\text{Towns})}, \rho_{(\text{Water})}$	195.21	12.92	<0.01
	$\Psi_{(\text{TreeHeight})}, \rho_{(\text{Water})}$	195.31	13.02	<0.01
	$\Psi_{(\text{VPC})}, \rho_{(\text{Water})}$	195.32	13.03	<0.01
	$\Psi_{(\text{Slope})}, \rho_{(\text{Water})}$	195.38	13.09	<0.01
	$\Psi_{(\text{CanopyCover + VPC})}, \rho_{(\text{Water})}$	195.79	13.50	<0.01
	$\Psi_{(\text{CanopyCover + Slope})}, \rho_{(\text{Water})}$	196.57	14.28	<0.01
	$\Psi_{(\text{CanopyCover + VPC + Slope})}, \rho_{(\text{Water})}$	197.60	15.32	<0.01
	$\Psi_{(.)}, \rho_{(.)}$	201.88	19.59	<0.01

[a] *AIC* Akaike information criterion

[b] *AICwt* weight of Akaike information criterion

at the four cardinal points with a 2 m × 5 cm ruler divided into 10 sections of 20 × 5 cm alternately painted in black and white. The ruler was placed vertically at one point and the number of sections visible at 15 m was counted. The difference between the observed number of sections and the total number of sections (10) expressed as a percentage was considered as the percentage of coverage protecting pacas from their predators (Griffith and Youtie 1988). The percentage of slope (Slope) was determined using a clinometer, making readings toward the four cardinal points of each sampling station (Ortiz-Martínez et al. 2005).

8.2.4 Data Analysis

Once all the photographs were obtained, paca photographs were selected and imported into the Camera Base program (Tobler 2007), where the independent records were separated. The following were considered independent photographic records: (1) consecutive photographs of individuals of different species; and (2) consecutive photographs of the same species separated by 24 h. In photographs where several individuals of the same species or different species appeared, the records were considered as the total number of individuals captured (Monroy-Vilchis et al. 2011).

To explore the influence of habitat structure on paca occupancy probability (Ψ), the models Single-Species and Single-Season were constructed (MacKenzie et al. 2002) using the Unmarked package (Fiske and Chandler 2011) in the R program (R Core Team 2019). Before the construction of the models, Pearson's product–moment correlation coefficient was calculated (r, Table 8.1) to examine the correlates among the covariates at the site level. Uncorrelated variables ($|r| < 0.60$) and with inflation factor of variance (VIF < 4 values; Naimi et al. 2014) were grouped and combined for the construction of the different models. The variables were standardized (mean zero and standard deviation of 1) with the R package Vegan (Oksanen et al. 2013).

Detection histories were constructed showing whether a paca was detected (1) or not (0) across the two monitoring seasons, rainy in 2017 (Rainy_{2017}) and dry in 2018 (Dry_{2018}). Each sampling occasion consisted of the grouping of 10 days to reduce the number of occasions without detections in the capture history, resulting in 22 sampling occasions in the rainy season and 17 in the dry season.

The two-step approach proposed by MacKenzie et al. (2006) was used to build the final model. First, the candidate models for the detection process (ρ) were adjusted while the occupancy probability (Ψ) was fixed as a constant, and the most informative potential habitat covariates were used. The best model was selected using its AIC (Akaike Information Criterion) values. Secondly, the occupancy model was built by running all possible combinations of occupancy covariates with detectability constrained to the most important variables identified in step one. The best models were selected using the AIC to identify the final model. All models with a value of $\Delta\text{AIC} < 2$ were considered equivalent (Burnham and Anderson 2004) and model averaging was used to generate estimates for parameters of interest as implemented in the R package MuMIn (Burnham and Anderson 2002). The goodness of fit for the final model was evaluated using the *mb.gof.tests* function in the R AICcmodavg package (MacKenzie and Bailey 2004) with 5000 replicates. The estimated detection and occupancy values of the best model were calculated using the *BackTransform* function in the R Unmarked package (Fiske and Chandler 2011).

8.3 Results

The sampling effort was 4822 camera-days, of which 2746 corresponded to the rainy season and 2074 to the dry season. A total of 202 independent paca records were obtained (96 records in the rainy season and 106 in the dry season). There was no correlation between habitat covariates and none of the variables showed VIF values greater than 4 (Table 8.1). Therefore, all variables were used to model the occupancy and detection probabilities of the paca.

The model selection process resulted in 14 candidate models for the paca occupancy probability in the rainy season and 18 models for the dry season (Table 8.2). The best candidate model for the rainy season was $\Psi_{\text{(Canopy Cover)}}$, $\rho_{\text{(Water)}}$; however, the first six models had AIC < 2 and used average estimates of occupancy with the highest weight of 0.41, while in the dry season, the best model was $\Psi_{\text{(Water + CanopyCover + VPC)}}$, $\rho_{\text{(Water)}}$ with a weight of 0.78. The paca detection probability varied between seasons. It was 0.26 ± 0.03 in the rainy season, while it was 0.36 ± 0.04 in the dry season. Detection was negatively influenced by distance to water bodies in both seasons ($\beta = -0.71$; CI: -1.14 to -0.27).

The probability of paca occupancy in the rainy season ($\Psi = 0.84 \pm 0.1$) had a weak positive relationship with canopy coverage ($\beta = 1.49$; CI: 0.69–3.67), whereas in the dry season ($\Psi = 1 \pm 0.15$) it had a negative and weak relationship with distance to water bodies ($\beta = -6.57$; CI: -23.04 to -2.24). Paca occupancy also had a positive but weak relationship with vertical protection coverage ($\beta = 16.1$; CI: 6.6–28.80) and canopy coverage ($\beta = 4.36$; CI: 4.11–15.12). The goodness of fit for the best model in the rainy season was low ($\hat{c} = 0.06$, $p = 0.45$), suggesting a well-fitting model. For the dry season, the goodness of fit of the best model was moderated ($\hat{c} = 0.32$, $p = 0.48$), showing a moderately underdispersed model.

8.4 Discussion

The paca detection probability was closely related to the presence of water bodies. This is one of the most important resources for pacas since the proximity to water bodies represents an alternative to escape from their predators and allows them to meet a physiological requirement for defecation (Pérez 1992; Muñoz et al. 2002; Trujillo et al. 2005; Goulart et al. 2009; Parroquin et al. 2010; Figueroa de León et al. 2016; Harmsen et al. 2018). In Neotropical forests, the sleeping and resting places of this species are close to water bodies (Aquino et al. 2009). Likewise, paca detectability decreases as the distance to water resources increases (Ferreguetti et al. 2018).

The probability of paca occupancy in both seasons was related to canopy coverage. A greater canopy coverage can decrease the possibility of being detected by a predator when feeding since a greater coverage prevents moonlight penetration and reduces predation risk for pacas (Parroquin et al. 2010; Pratas-Santiago et al. 2017). In addition, a greater number of burrows has been reported in habitats with a dense vegetation cover (Parroquin et al. 2010). In the dry season, paca occupancy probability is also related to vertical protection coverage. This confirms that protection from predators seems to be a determining factor in habitat selection by pacas (Ecke et al. 2002; Ortiz-Martínez et al. 2005). Another covariate related to paca occupancy probability in the dry season was the distance to water bodies. Ferreguetti et al. (2018) found that paca occupancy probability increased as distance to water decreased in Brazil's Atlantic Forest, and Figueroa de León et al. (2016) found an increased probability of cavity occupancy in slopes along rivers and streams. It has been observed that water bodies like rivers or streams facilitate the escape of pacas from their predators: when they are chased or threatened, they throw into the water and can remain submerged for a long time (Muñoz et al. 2002).

Pacas prefer areas with greater vegetation cover, as well as places close to water resources. However, it is necessary to evaluate other elements that could potentially affect paca occupancy in the Sierra Norte de Oaxaca such as the presence of predators, hunting pressure, and food availability (Figueroa de León et al. 2017; Santos-Moreno and Pérez-Irineo 2013). Although there is evidence that the paca is tolerant to habitat modification (Gallina et al. 2012), it has also been observed that this species may be vulnerable to fragmentation processes (Ojasti 1993; Rodríguez 1994). Consequently, it will be important to examine the vulnerability of the species to human activities. In this sense, this study allowed understanding important aspects of paca ecology. Habitat occupancy of the paca has been barely assessed using hierarchical methods; this study presents one of the first estimates in Mexico and in the Neotropics. This knowledge is fundamental for developing effective conservation strategies for this species, which is key to the regeneration and maintenance of the plant communities in which it lives.

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Chapter 9
Jaguars (*Panthera onca*) in the Llanos of Colombia and Venezuela: Estimating Distribution and Population Size by Combining Different Modeling Approaches

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Abstract The Llanos of Colombia and Venezuela are an ecoregion composed of savannas, forests, and wetlands, with a high biodiversity and once home to a high-density jaguar (*Panthera onca*) population. We used published and new jaguar presence–absence data from 2001 to 2020 and combined logistic regression with kriging interpolation to model jaguar occurrence and estimate its current range in the Llanos. Water abundance, forest cover, and primary productivity had positive

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effects, while road density had a negative effect in the model. The jaguar's estimated current range covers 49% of the total area of the Llanos. This estimate is 45% and 16% lower than the 2000 and 2015 IUCN Red List assessments, respectively. We combined a previously published density model with our occurrence model to estimate the variation in jaguar population density and its population size. In most of the Llanos area, projected densities ranged from 1 to 3 jaguars per 100 km^2, and we estimated the total population at 3413 jaguars (CRI: 2525–4272), two-thirds in Venezuela and one-third in Colombia. Human–jaguar conflict records, mostly jaguar attacks on livestock, were widespread on the Llanos but tend to occur at moderate cattle density and higher forest cover. In 49% of the conflict records, jaguars were killed in retaliation; however, 25% of the nonconflict records also reported killing jaguars during subsistence hunts. Protected areas and indigenous territories cover only 10% and 4% of jaguar's estimated current range, respectively, indicating an urgent need to increase the number and extent of protected areas in the Llanos.

Keywords Carnivore conservation · Distribution changes · Illegal hunting · Jaguar population decline · Kriging interpolation · Population density · Retaliatory killing · Species assessments · Species distribution models

9.1 Introduction

The Llanos, also known as Orinoco Llanos, is a large (440,000 km^2) and unique ecological system southeast of the Andes in Colombia and Venezuela. It is a natural mosaic of grassland savannas, forests, shrublands, swamps, and floodplains with numerous rivers, today densely interspersed with cattle pastures and agricultural fields (Figs. 9.1, 9.2, 9.3, 9.4, and 9.5). This ecoregion has high primary productivity and provides habitat for rich bird, reptile, and mammal communities.

The Llanos is an important jaguar habitat, ecologically similar to the Pantanal in Brazil. Jaguars (*Panthera onca*) in the Llanos live in the forest-wetland mosaic (Fig. 9.6), where they mainly prey on white-lipped peccary (*Tayassu pecari*), collared peccary (*Dicotyles tajacu*), capybaras (*Hydrochoerus hydrochaeris*), spectacled caimans (*Caiman crocodilus*), and white-tailed deer (*Odocoileus virginianus*) (Figs. 9.7, 9.8, 9.9, 9.10, and 9.11), but also on a variety of smaller prey and cattle (Crawshaw and Quigley 2002; Polisar et al. 2003; Scognamillo et al. 2003; Perilli et al. 2016).

The natural prey biomass is usually high, and it is further increased by numerous cattle herds (Figs. 9.12, 9.13 and 9.14). For example, in Hato Piñero, a partially protected ranch in the Venezuelan Llanos, Polisar et al. (2003) estimated 750 kg/km^2 of natural prey and 7700 kg/km^2 of livestock as potential prey resources for jaguars, which is a higher estimate than the biomass estimated for Pantanal (380 kg/km^2 of natural prey, Schaller 1983). Under these conditions, jaguar populations in the Llanos reach high density. In Hato Piñero, where there is no hunting, the jaguar density is estimated at 4.4 adults and 3.2 cubs per 100 km^2 (Jędrzejewski et al. 2017c), which is among the highest throughout the jaguar range. However, in less

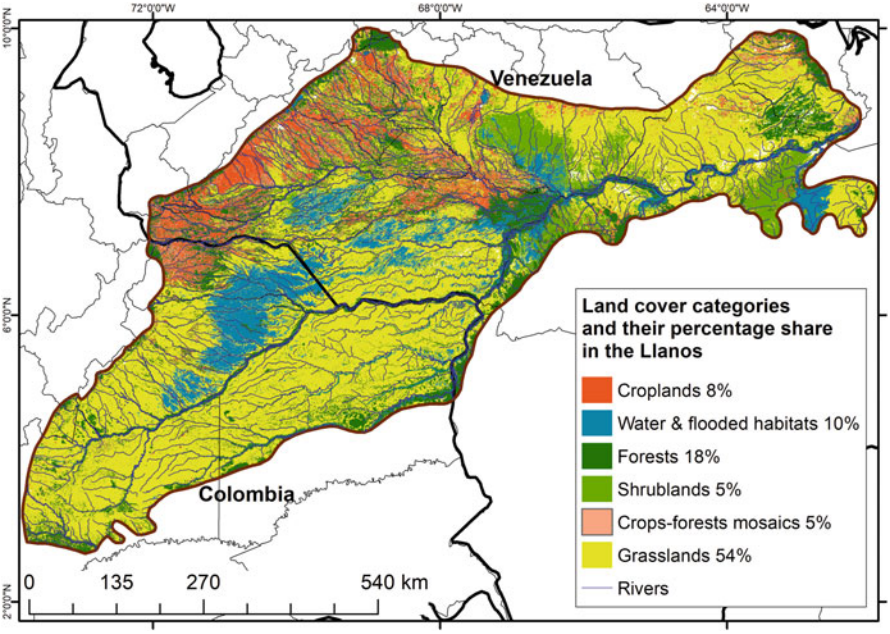

Fig. 9.1 The main land cover categories found on the Llanos today (2020), according to Land Cover CCI data; https://maps.elie.ucl.ac.be/CCI/viewer/index.php

Fig. 9.2 The Llanos is a habitat mosaic composed of natural grasslands, wetlands, and forests. Venezuelan Llanos (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.3 There are numerous rivers and streams inside the forested areas in the Llanos. Hato Piñero, Cojedes, Venezuela (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.4 Cinaruco river. Apure state, Venezuela (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.5 Natural savannas used as pastures in the Venezuelan Llanos. Cojedes state, Venezuela (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.6 Riversides are one of the preferred habitats of jaguars in the Llanos. Hato El Frio, Apure state, Venezuela. Camera trap (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.7 The white-lipped peccary (*Tayassu pecari*) is often abundant in the forests and together with the collared peccary (*Dicotyles tajacu*) are often hunted by jaguars in the Llanos. Hato Piñero, Cojedes, Venezuela. Camera trap (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.8 Capybaras (*Hydrochoerus hydrochaeris*) are important jaguar prey in the Llanos. They feed on the water plants or they graze around the water bodies, always escaping to the water when in danger. Hato Aurora, Colombian Llanos (Photo credit: Valeria Boron)

Fig. 9.9 Grazing capybaras (*Hydrochoerus hydrochaeris*) in Hato Piñero, Venezuelan Llanos (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.10 Groups of the spectacled caiman (*Caiman crocodilus*), one of the important jaguar prey, aggregate in the water bodies during the dry season. Hato Piñero, Cojedes state, Venezuelan Llanos (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.11 White-tailed deer (*Odocoileus virginianus*) is very abundant in the Llanos and is a common supplementary prey for jaguars. Hato Piñero, Cojedes state, Venezuelan Llanos (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.12 Natural, seasonally flooded grasslands are often used as pastures in the extensive cattle ranching in the Venezuelan Llanos. Hato Piñero, Cojedes state (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.13 Sanmartinero cattle extensively managed in the Casanare state, central Colombian Llanos (Photo credit: Rafael Hoogesteijn)

Fig. 9.14 Extensive cattle ranching on the recently deforested areas in Barinas state, Venezuelan Llanos (Photo credit: Włodzimierz Jędrzejewski)

protected areas of Hato Aurora in the Colombian Llanos, where jaguars and their prey are often hunted, the jaguar density was estimated at only 1.9 adult jaguars/ 100 km^2 (Boron et al. 2016).

Jaguars from the Llanos, together with the Pantanal jaguars, reach the largest body size among all jaguar populations; males can weigh up to 130 kg, and they are significantly larger and heavier than jaguars from the more forested habitats of South or Central America (Hoogesteijn and Mondolfi 1996). The Llanos and Pantanal jaguars also show similar behavior: only in these two populations, male–male coalitions and male–male collaborative behavior presumably intended to increase reproductive success have been reported (Jędrzejewski et al. 2022).

In pre-Columbian times, the Llanos were populated by various indigenous groups, some specialized in agriculture or fishing, and others in hunting and gathering. However, they were mostly nomadic and their impact on the environment was probably low. After the settlement of European colonizers, most of these groups were exterminated and only a few survived by the seventeenth century (Arellano 1986; Méndez-Echenique 1995). Vast natural savannas with rich soils and diversity of grass species stimulated a fast development of cattle ranching and some agriculture. Cattle breeding began in the sixteenth century and was widely developed already in the eighteenth century in the Llanos (Huertas-Ramírez and Huertas-Herrera 2015). Until 1950, however, the Llanos were poorly accessible and thus remained sparsely populated and largely unchanged (Giacopini-Zarraga 1992). Consequently, jaguars were abundant and widespread in the Llanos (Sanderson et al. 2002a), likely reaching very high densities. Several reports from the 1950s on jaguar hunting in the Venezuelan Llanos suggest a high abundance of jaguars in those times. For example, in Hato Cordereño (1300 km^2, Barinas state), a group of few hunters with dogs shot 43 jaguars in only three months (Hoogesteijn and Mondolfi 1992).

Although the Llanos are usually associated with open habitats, originally vast, highly diverse tropical forests covered much of their area. After 1950, large-scale deforestation and conversions of forests to pastures or agriculture took place, with a peak between 1970 and 2000. For example, between 1975 and 1988, over 18,000 km^2 were deforested in the western Venezuelan Llanos (Pacheco et al. 2011). Large natural areas are currently being transformed. In some of them, particularly in the west of the region, a dense network of roads was constructed. Livestock, especially cattle, and rice production are important economic activities in the Venezuelan Llanos. The Colombian Llanos, apart from the intensive cattle ranching, are also subjected to petrol extraction, deforestation, and other large-scale habitat transformations (Figs. 9.1 and 9.15) aimed at rice, soybean, and oil-palm production (Mora-Fernández and Peñuela-Recio 2013).

Despite the high abundance of jaguars throughout the Llanos during the first half of the twentieth century (Sanderson et al. 2002a), their populations substantially declined during the last 70 years. The largest reduction in the jaguar range between 1970 and 2000 coincided with the highest rates of deforestation, suggesting that habitat changes were the major driver of the jaguar decline (Pacheco et al. 2011, Jędrzejewski et al. 2017a, 2023a). Jaguar killings, second in importance in

Fig. 9.15 Newly established plantation of oil palm – an example of large-scale habitat transformations in the Colombian Llanos (Photo credit: Rafael Hoogesteijn)

explaining jaguar declines, increased after 1950 (Giacopini-Zárraga 1992). The fast development of cattle ranching triggered jaguar predation on cattle and retaliatory killings by ranchers. Moreover, the publicized cases of livestock predation by jaguars motivated opportunistic and sport hunters to intensify jaguar hunting (Velutini 1978; Giacopini-Zárraga 1992; Hoogesteijn and Mondolfi 1992; Hoogesteijn et al. 1993, 2002). Additionally, jaguar pelts became fashionable in Europe and North America triggering an increase in fur prices and in the intensity of jaguar hunting all over South America through the 1960s and 1970s (Hoogesteijn and Mondolfi 1990a, b, 1992, Payán and Trujillo 2006, Jędrzejewski et al. 2017a, b).

Today, complex factors influence jaguar persistence in the Llanos. Jaguars are legally protected in both Colombia and Venezuela, and the legal trade of jaguar skins ceased thanks to the enforcement of CITES regulations (Kretser et al. 2022; Payan et al. 2023). However, habitat continues to deteriorate, particularly due to deforestation, conversion of natural savannas to pastures and agriculture (Fig. 9.15), and road expansions (Pacheco et al. 2011, 2014; Mora-Fernández and Peñuela-Recio 2013, Payan et al. 2013, IDEAM 2019; Payan and Boron 2019; Jędrzejewski et al. 2023a, b). In addition, jaguar killings due to conflicts between jaguars and ranchers (Figs. 9.16 and 9.17) or due to subsistence hunting (Fig. 9.18) are widespread (González-Fernández 1995; Hoogesteijn et al. 2002; Jędrzejewski et al. 2017a, b). Compared to the Amazon or other regions, the area under protection remains very

Fig. 9.16 Jaguars often attack livestock which may lead to a conflict with ranchers and cause retaliatory killing of the jaguar. Hato Piñero, Venezuelan Llanos (Photo credit: Włodzimierz Jędrzejewski)

Fig. 9.17 Ranchers often kill jaguars in retaliation, when jaguars attack cattle or as a preventive measure, when jaguar tracks are located inside a ranch. Venezuelan Llanos (Photo credit: Rafael Hoogesteijn)

Fig. 9.18 Across the Llanos there are also numerous subsistence hunters who occasionally may kill a jaguar during a chance encounter while hunting other game species. However, some of them may intentionally track jaguars and kill them for skin, fangs, and meat (Jędrzejewski et al. 2017b). Guárico, Venezuela (Photo credit: Włodzimierz Jędrzejewski)

small; protected areas cover only 6%, and indigenous territories an additional 3% of the total Llanos area (RAISG 2020). There are also important differences in the economic development between Colombia and Venezuela, which may influence the jaguar's interaction with humans and the rate of habitat degradation in the Llanos. While Colombia has been developing rapidly in recent decades, Venezuela has experienced a major political crisis that has resulted in an economic slowdown, a decline in production, insecurity, and a high emigration rate: between 2016 and 2022, over seven million people left Venezuela (ACNUR 2022).

In this chapter, we analyze the current population status of jaguars and the factors shaping the probability of their occurrence in the Llanos of Venezuela and Colombia. We tested the hypothesis that key environmental factors related to the occurrence and abundance of jaguars' main prey in the Llanos will drive the occurrence of jaguars, while all human-induced environmental changes lead to their disappearance. We used a general hierarchical modeling framework in which we combined logistic regression and kriging interpolation to estimate the current jaguar distribution and then combined these results with a previously published jaguar population density model to estimate the jaguar population size in the Llanos of Venezuela and Colombia. For this analysis, we used specific predictor variables adjusted to the region-specific characteristics of jaguar ecology and the climatic, habitat, and land-use features prevalent in the region. We also analyzed available data on jaguar predation on cattle and jaguar mortality to evaluate the importance of human–jaguar conflict for jaguar persistence.

9.2 Methods

9.2.1 Study Area

We have adopted the boundaries and division of the Llanos ecoregion according to Griffith et al. (1998) who based their classification on natural vegetation types, geology and physiography, climate, and land use. The main vegetation types in the Llanos include vast areas of savanna-type grasslands (54%), various types of forests (18%), open or partially open wetlands and water bodies (10%), croplands (8%), shrublands (5%), and mosaics of small croplands, pastures, and forests (5%) (Fig. 9.1). Large areas of former natural grasslands and other habitats have been converted to cattle pastures and agriculture. Several major rivers and a dense network of smaller streams and canals intersect the whole region (Fig. 9.1). The climate is strongly seasonal, with most rainfall and extensive flooding occurring between April and November. The eastern Llanos receive less precipitation and have less flooding than the central and western Llanos (de Stefano et al. (2007). Griffith et al. (1998) distinguish three sub-ecoregions within the Orinoco Llanos: (1) Piedmonts, (2) High Plains and Dissected Plains, (3) Alluvial Overflow Plains, Wet Plains, and Flooded Plains. The region has a relatively high density and biomass of potential prey species for jaguars, including capybaras, caimans, peccaries, white-tailed deer, various species of turtles, and livestock, mostly cattle (Polisar et al. 2003).

9.2.2 Data Collection and Analysis

We used published (Jędrzejewski et al. 2017a, b, 2018, 2023a) and unpublished data on jaguar presence and absence in the Llanos from 2001 to 2020. To obtain presence data, we used jaguar records collected mostly with camera trapping, radiotracking, recording of tracks, and field interviews. Absence points came from field interviews and long-term camera trapping studies. We thinned out clumped data points, allowing a maximum of one record per each 100 km^2 to avoid the negative effects of spatial autocorrelation (Segurado et al. 2006; Dormann et al. 2007; de Angelo et al. 2011). To get a balance between the presence and absence points, we randomly selected the missing number of random points from the known jaguar absence areas (based on Quigley et al. 2018) where jaguars have not been reported recently. The total number of available jaguar records from 2001 to 2020 was 1200 and that of confirmed jaguar absence points was 300. However, after thinning out densely distributed points to only one per 100 km^2, we used for the analysis 214 jaguar records and 163 confirmed absence points. Additionally, we selected 37 random absence points from the areas of known jaguar absence.

To estimate the distribution and abundance of jaguars in the Llanos, we used a general hierarchical modeling approach where we combined different models to improve their performance. To determine the current distribution of the jaguar population we combined logistic regression with the kriging interpolation technique (Jędrzejewski et al. 2017a). Logistic regression is commonly used to estimate probabilities of species occurrence based on the relationship between presence and absence data and a set of predictive variables (Elith and Leathwick 2009). Kriging interpolation is a geostatistical method based more directly on the distribution of presence and absence points and applied to estimate species distribution when data are spatially autocorrelated (Monestiez et al. 2006; Hengl et al. 2009; Nazeri et al. 2015). We combined these two methods to improve our estimate of jaguar distribution in the areas where logistic regression alone predicts different results than the actual distribution of presence/absence points (Jędrzejewski et al. 2017a), which for example may occur in highly fragmented jaguar habitats surrounded by anthropogenic areas, the situation often found in the Llanos.

In the case of logistic regression, we fitted a set of models to presence–absence data from the Llanos. Candidate predictive variables (see Table 9.6, supplementary material) included the following groups: (1) long-term means of annual precipitation and daily temperature; (2) long-term means and standard deviations of five vegetation indices obtained from satellite images related to vegetation abundance and primary productivity (NPP, GPP, NDVI, EVI) and with water content in the leaves and in the ground (NDWI); (3) canopy (percentage of area covered with trees); (4) proportions of area (in each 1 km^2) covered by four land use categories: croplands, grasslands, forests, and water/flooded areas; (5) human population density; (6) road density index; (7) Human Footprint index; (8) protected areas; and (9) spatial division to three sub-ecoregions of the Llanos as defined by Griffith et al. (1998), in relation to our presence–absence data location (Table 9.6, supplementary material). We used mean values of climatic and vegetation productivity indices because they determine the density and productivity of herbivores, the potential prey of jaguars, and their standard deviations because they are measures of seasonality and are also related to densities of herbivores and carnivores (Polisar et al. 2003; Karanth et al. 2004; Melis et al. 2009; Pettorelli et al. 2011). We tested for multicollinearity in our models by calculating tolerance and variance inflation factor (VIF) for each of the predictive variables. We eliminated variables with tolerance lower than 0.25 or VIF higher than 4, except the variables that entered the model with their quadratic terms (Hosmer et al. 2013). We selected the best model using the Akaike Information Criterion AIC (Burnham and Anderson 2002). We also calculated Nagelkerke's R-Square, the area under the receiver operating characteristic curve (AUC) and produced a classification table to evaluate how the model fits the data (Nagelkerke 1991; Hosmer et al. 2013). We converted the logit values obtained from the best model to the probability of jaguar occurrence and made spatial predictions at the same resolution (1 km^2). All model fitting was conducted using SYSTAT 13.2 (Systat Software, Inc., San Jose, CA, USA) and JASP (JASP Team, 2022, University of Amsterdam).

We used the kriging interpolation function within ArcGIS 10.4 and calculated a spatial prediction of the probability of jaguar presence by interpolating all jaguar presence and absence records. Within ArcGIS, we applied ordinary kriging, the spherical semivariogram model, and the six nearest points to calculate values for each raster cell (1 km^2). We also calculated the kriging variance for each cell. Higher values of kriging variance are related to a low density of data points and should not be used for predicting species distribution (Heuvelink and Pebesma 2002). To avoid incorrect predictions of kriging interpolation along the borders of the Llanos, we also used published jaguar presence–absence data from outside of the Llanos (Jędrzejewski et al. 2018).

To estimate the current jaguar distribution in the Llanos, we used different procedures for areas for which we had presence/absence points than for areas where we had no data and for which we obtained higher values of kriging variance. To simplify the procedure, we created quadratic buffers of 50 × 50 km around each data point. Inside the joint area of these buffers, we averaged the probabilities of jaguar occurrence obtained with both the logistic regression and kriging models and we selected areas with mean probabilities higher than 0.5 as presence areas (jaguar current range) and areas with lower probabilities as absence areas (Jędrzejewski et al. 2017a). Outside the combined buffer area, we used the prediction of the best logistic regression model alone to distinguish between the jaguar presence and absence areas, using the same probability threshold values as above. We produced a confusion matrix and calculated the proportion of correctly classified presence and absence points ("sensitivity" and "specificity," respectively) as well as AUC values to verify if this combined method fitted better to data points than single models.

We estimated the size of the jaguar population in the Llanos by combining density and distribution models, following the general approach proposed by Jędrzejewski et al. (2018). We multiplied the potential jaguar population densities by the probabilities of jaguar occurrence that we obtained here to get corrected density predictions. The potential jaguar densities were estimated by Jędrzejewski et al. (2018) with the regression model based on 110 published jaguar density estimates and a set of predictive environmental variables that included mean and standard deviation of net primary productivity and mean annual temperature, but not included any factors related to human impacts. By combining the potential density and the occurrence model that included anthropogenic factors we adjusted jaguar density estimates to the actual habitat condition and changes resulting from human impacts (Jędrzejewski et al. 2018). To estimate the jaguar population size, we summed up the corrected jaguar population densities for each 1 km^2 cell within the area of our estimate of the current jaguar range. To evaluate the uncertainty of our estimates we calculated the 95% lower and upper credible limits, applying respective percentage credible intervals for Colombia and Venezuela that were estimated with Markov Chain Monte Carlo iterations by Jędrzejewski et al. (2018).

For the analysis of human–jaguar conflicts and human-caused jaguar mortality in the Llanos, we excluded from our dataset the camera trap data and we used 326 jaguar records obtained with interviews conducted in the field, without thinning out the densely distributed data. These included conflict records (jaguar attacks on livestock and a few jaguar attacks on humans) and nonconflict records, such as incidental sightings of jaguars in forests or jaguar attacks on wild animals. Within both conflict and nonconflict records we further distinguished between records that ended up in jaguar killing vs. records that did not.

9.3 Results

9.3.1 Habitat Suitability, Jaguar Distribution, and Current Status

The best logistic regression model of jaguar presence and absence included seven variables with positive effects: NDWI-mean, Flooded and Water Areas, Precipitation, GPP-mean, Forest Canopy Cover, Protected Areas, and NDVI-standard deviation. Two variables had negative effects: Human Footprint and Road Density. The model also included three variables with quadratic terms (Temperature, Croplands, and Cattle) indicating a nonlinear effect of these variables with some range of positive impacts. In addition, it contained the categorical variable representing the division of the Llanos into three sub-ecoregions (Table 9.1). This model had fairly good predictive power ($p < 0.001$, AUC = 0.873, Nagelkerke's $R^2 = 0.52$, sensitivity = 0.80, specificity = 0.77, accuracy = 0.79). The spatial prediction of our model showed a highly fragmented, mosaic distribution of suitable and unsuitable jaguar habitats in the Llanos (Fig. 9.19a). The central part of the Llanos has generally better habitats for jaguars than the eastern and western parts. However, across the Llanos jaguar, actual records and absence points are often mixed up with each other, with numerous records found in the areas of low suitability as well as local absence points within habitats highly suitable for jaguars (Fig. 9.19a).

Table 9.1 The parameters of the best logistic regression model of jaguar presence and absence in the Llanos

Parameter	Estimate	Standard error	*Z*	*p*
(Intercept)	−219.4075	96.3913	−2.28	0.0228
Normalized difference water index NDWI (mean)	20.7033	5.2137	3.97	<0.001
Water bodies and flooded habitats (%)	4.4577	1.2832	3.47	<0.001
Mean annual precipitation	0.0012	0.0004	2.92	0.0035
Gross primary productivity GPP (mean)	0.0115	0.0042	2.72	0.0065
Forest canopy cover (%)	0.0342	0.0127	2.69	0.0071
Protected areas	1.7272	0.6452	2.68	0.0074
Normalized difference vegetation index NDVI (SD)	13.4302	5.5406	2.42	0.0154
Human Footprint Index (2004)	−0.0727	0.0175	−4.15	<0.001
Road density index	−3.0794	0.9190	−3.35	<0.001
Mean daily temperature	16.6977	7.1765	2.33	0.0200
Mean daily temperature (squared)	−0.3178	0.1336	−2.38	0.0174
Agricultures (%) (squared)	−3.0677	1.1914	−2.57	0.0100
Cattle density (squared)	−0.0008	0.0004	−2.02	0.0431
Sub-ecoregion division of the Llanos	−0.4019	0.1854	−2.17	0.0302

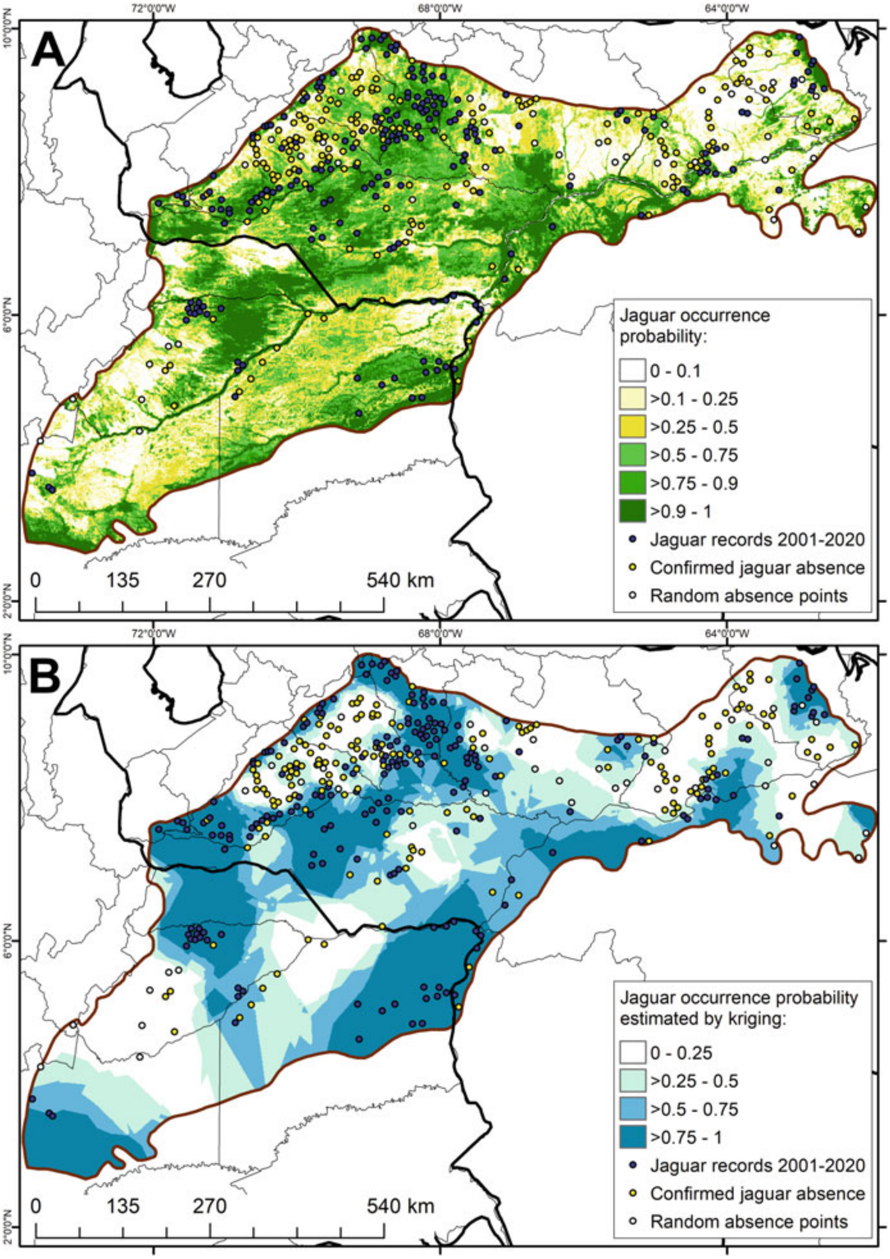

Fig. 9.19 Results of our modeling of jaguar occurrence probabilities. (**a**) Spatial prediction of our best logistic regression model. (**b**) Results of the kriging interpolation of presence (= 1) and absence (= 0) data points

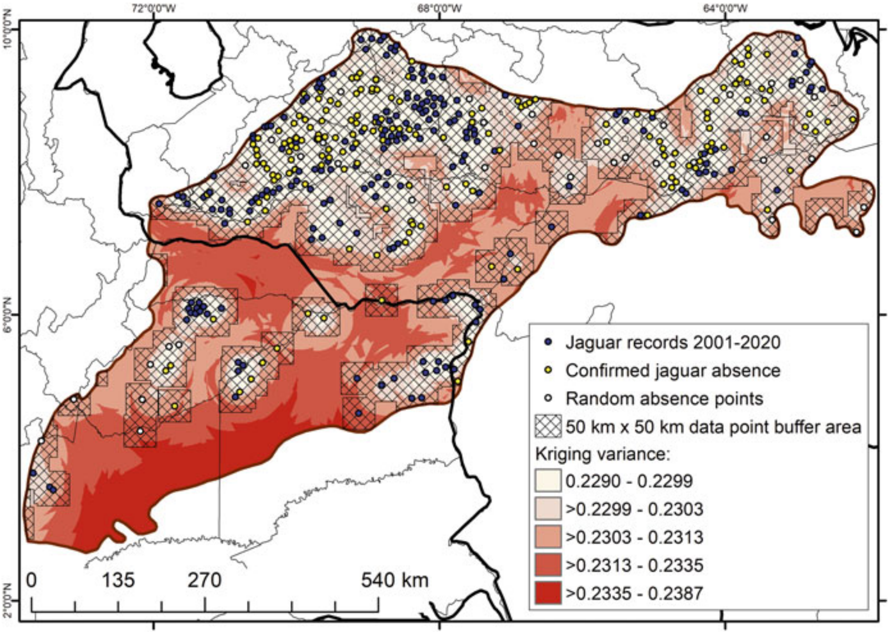

Fig. 9.20 Kriging variance resulting from kriging interpolation of our jaguar presence–absence data. For areas of lower variance, approximated by a combined 50 × 50 km buffer around each data point, we used the combined results of logistic regression and kriging interpolation to estimate the jaguar's current range, while for areas of higher variance, outside of the buffer, we used only projections from the logistic regression model

The kriging interpolation produced a similar spatial prediction of jaguar occurrence probabilities (Fig. 9.19b) with an even better fit to the data points (AUC = 0.932, sensitivity 0.89, specificity 0.84). However, outside of the areas covered by our data, the kriging prediction was characterized by high kriging variance (Fig. 9.20) and spatial predictions for these areas were schematic and obviously unrealistic (Fig. 9.19b). Combining both models resulted in a good fit to the presence–absence data, with AUC = 0.928, sensitivity 0.91, and specificity 0.80 (Fig. 9.21). The jaguar's current range estimated with the combined models covers 214,000 km^2, that is 49% of the total area of the Llanos (Table 9.2). Compared to 2000 and 2015 IUCN estimates, there has been a significant decrease in the range of jaguars in the Llanos over the last 20 years (Table 9.2). The current jaguar's range in the Llanos is highly fragmented and vast areas do not have jaguars anymore (Fig. 9.21). The models indicated that jaguars are extinct in 56% of the area of the Colombian Llanos and in 49% of the area of the Venezuelan Llanos. A comparison of jaguar distribution with the land protection status demonstrates that protected areas cover only 10% of the jaguar's current range, and the indigenous territories only 4%, leaving 86% of the area occupied by the jaguar in the Llanos without legal protection (Fig. 9.22).

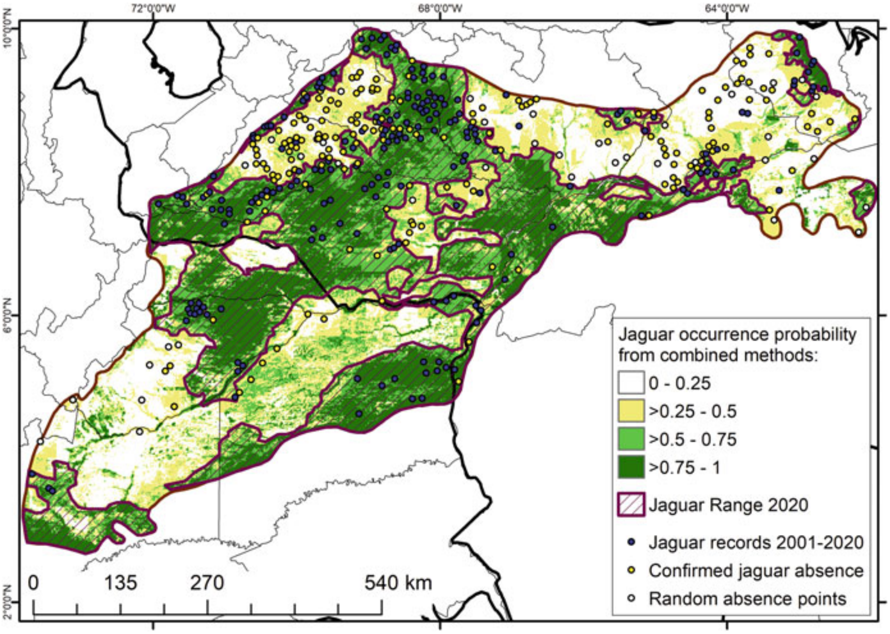

Fig. 9.21 Jaguar occurrence probability and jaguar's current range in the Llanos estimated with the combined logistic regression and kriging interpolation (at lower kriging variance) or logistic regression alone (at higher kriging variance, compare Fig. 9.20)

Table 9.2 Estimated area (in thousands km^2) of the current (2020) jaguar range in the Llanos compared to the IUCN estimates for 2000 and 2015 (Caso et al. 2008; Quigley et al. 2018)

Country	Total Llanos area	Jaguar range 2000 (IUCN)	Jaguar range 2015 (IUCN)	Jaguar range 2020
Colombia	174	152 (88)	151 (87)	77 (44)
Venezuela	267	263 (98)	136 (51)	137 (51)
Total Llanos	441	415 (94)	287 (65)	214 (49)

Respective percentages of the Llanos area are provided in parentheses

9.3.2 *Jaguar Population Densities and Population Size*

The potential jaguar densities predicted for each km^2 of the jaguar range in the Llanos using a density regression model (Jędrzejewski et al. 2018) ranged from 0.20 to 5.78 jaguars/100 km^2, with densities in most areas ranging from 1 to 3 jaguars/100 km^2 and an overall average of 2.16 jaguars/100 km^2 (Fig. 9.23a, Table 9.3). Predicted potential jaguar densities were slightly higher in Venezuela than in Colombia and corresponded well to the results of field studies (Table 9.3). The

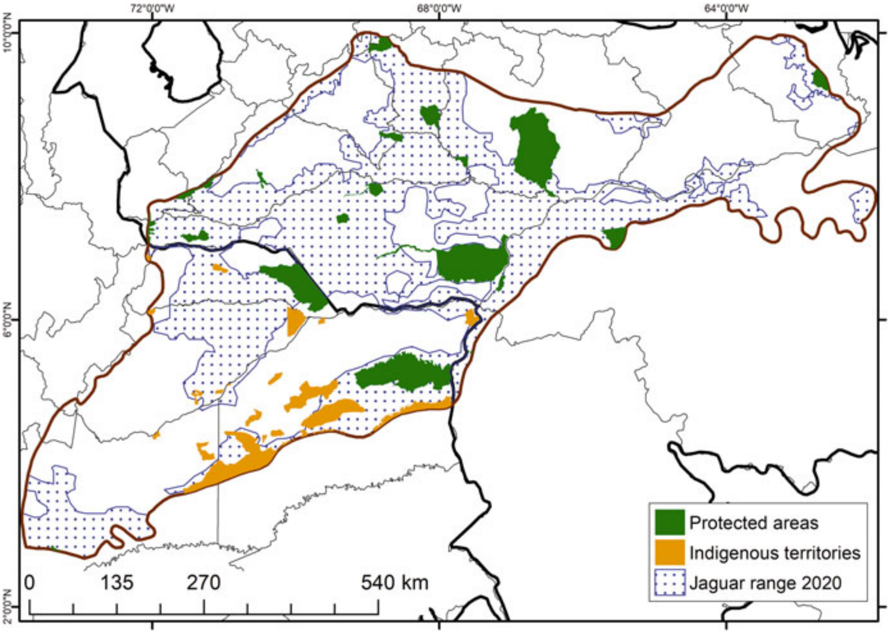

Fig. 9.22 Protected areas and indigenous territories in the Llanos, compared with our estimate of the jaguar's current distribution. Protected areas cover only 10% and indigenous territories only 4% of the area occupied by jaguars; however, official indigenous territories are found only in the Colombian part of the Llanos

corrected jaguar densities predicted by the combined density and distribution models (the latter taking human impacts into account) were much lower, with densities ranging from 1 to 2 jaguars/100 km^2 found in most areas, and an average of 1.61 jaguars/100 km^2 (Fig. 9.23b, Table 9.3). We estimated the jaguar population in its current range in the Llanos to be 3413 individuals (CRI: 2525–4272). Two-thirds of this population was found in Venezuela and one-third in Colombia (Table 9.3).

9.3.3 Human–Jaguar Conflicts and Jaguar Mortality

Our data on human–jaguar conflicts and jaguar mortality were mostly limited to the Venezuelan part of the Llanos because few interview data were available from the Colombian part (Figs. 9.24 and 9.25). Conflicts included mostly jaguar attacks on livestock (N = 156) and few jaguar attacks on humans (N = 4). Conflicts were widespread in the Llanos; however, at many localities, conflict records co-occurred with nonconflict records, such as incidental sightings of jaguars in forests or jaguar attacks on wild animals, and both types of records were mixed-up (Fig. 9.24). For this reason, we failed in constructing any robust model explaining the spatial

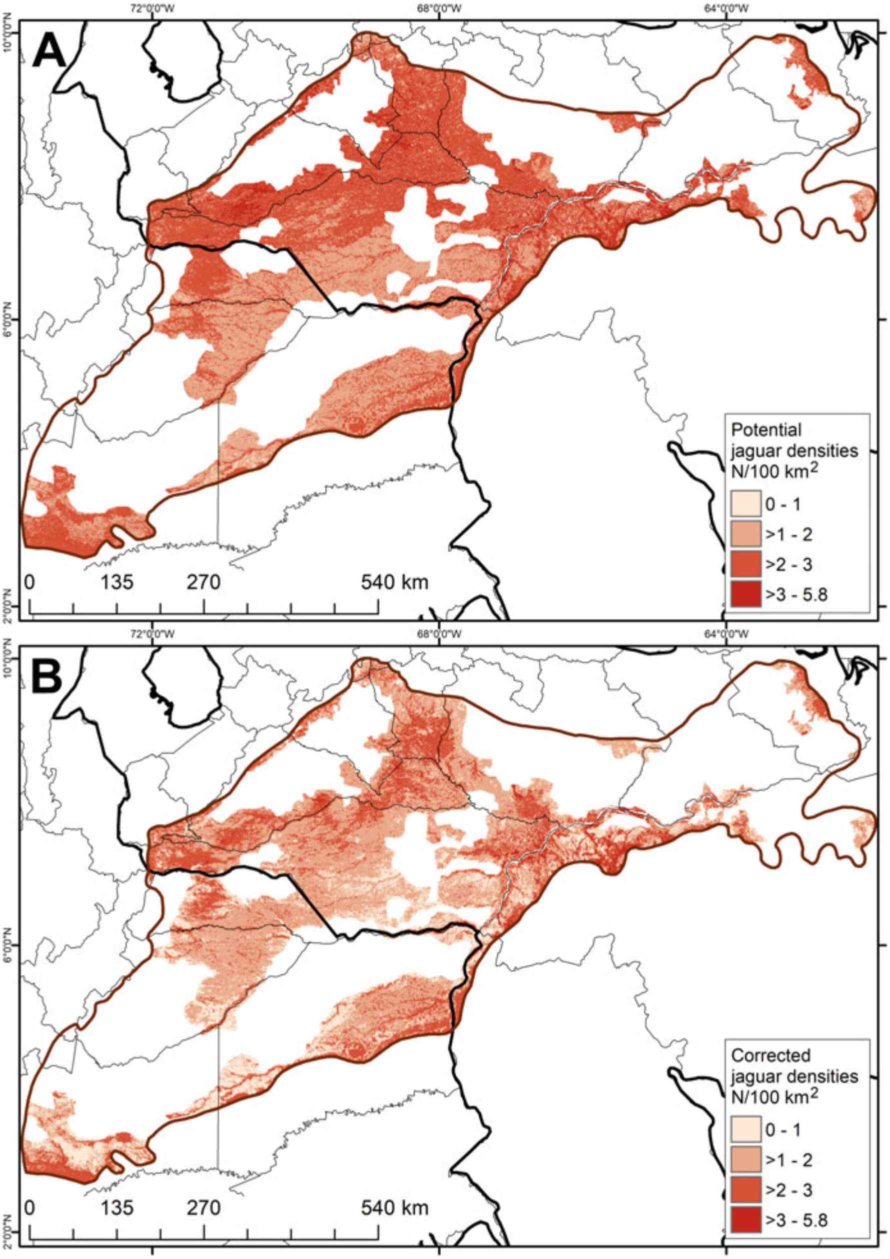

Fig. 9.23 (**a**) Jaguar potential densities within its current range predicted by a multiple regression model of jaguar population densities that included three environmental predictive variables: mean temperature and mean and standard deviation of net primary productivity derived from satellite images (Jędrzejewski et al. 2018). (**b**) Corrected jaguar population densities obtained by multiplying jaguar potential densities by probability of jaguar occurrence estimated with the combined methods (as in Fig. 9.21)

Table 9.3 Jaguar population density estimates from field studies, jaguar potential densities predicted by a density model, corrected jaguar densities that take into account current human impacts, and estimated jaguar population size in the Llanos

	Direct density estimates	Predicted potential densities	Predicted corrected densities	Total estimate of the jaguar population (CRI)
Venezuela	4.44	0.20–5.78 (2.19)	0.02–5.77 (1.70)	2319 (1753–2868)
Colombia	1.88	0.60–4.52 (1.91)	0.02–4.48 (1.47)	1094 (773–1405)
Total		0.20–5.78 (2.16)	0.02–5.77 (1.61)	3413 (2525–4272)

Jaguar population densities were directly estimated with camera traps and spatial capture–recapture models only in two studies in the Llanos: in Hato Aurora, Casanare, Colombia (Boron et al. 2016) and in Hato Piñero, Cojedes, Venezuela (Jędrzejewski et al. 2017c). Potential and corrected densities (range and mean of values predicted by models for each 1 km^2 raster cell) as in Fig. 9.23. Jaguar population size in the Llanos was estimated based on the corrected jaguar densities and the 95% credible intervals (CRI) were calculated based on percentage values provided by Jędrzejewski et al. (2018)

distribution of conflict and nonconflict records. Nevertheless, our data indicate that conflicts occurred mainly in areas characterized by medium values of forest cover and moderate values of cattle density, and their frequency distributions were statistically different from the percentage distributions of forest cover and cattle density within the jaguar's current range (Tables 9.4 and 9.5).

In 78 (49%) of the conflict records, jaguars were reported to be killed in retaliation. However, in 42 (25%) of nonconflict records, the jaguars were also reported to be killed in subsistence hunts. Both types of jaguar mortality records were widespread in the Llanos (Fig. 9.25), but records of retaliatory killing and subsistence hunting of jaguars had statistically different distributions in the classes of forest cover and cattle density (Tables 9.4 and 9.5). Interestingly, most records of conflicts and retaliatory killings occurred along the borders of the current jaguar range (Figs. 9.24 and 9.25).

9.4 Discussion

We estimated that jaguars still occur in about half of the Llanos area. A comparison with previous IUCN Red List assessments (Caso et al. 2008; Quigley et al. 2018) shows a significant decrease in jaguar distribution over the last 20 years. However, the former estimates were likely not accurate due to the lack of data, and they probably overestimated jaguar populations. Jędrzejewski et al. (2017a) showed that most jaguar extirpations in the Venezuelan Llanos occurred between 1970 and 1990. Nevertheless, our analysis shows that the jaguar's range is constantly decreasing and that it is a fairly rapid process.

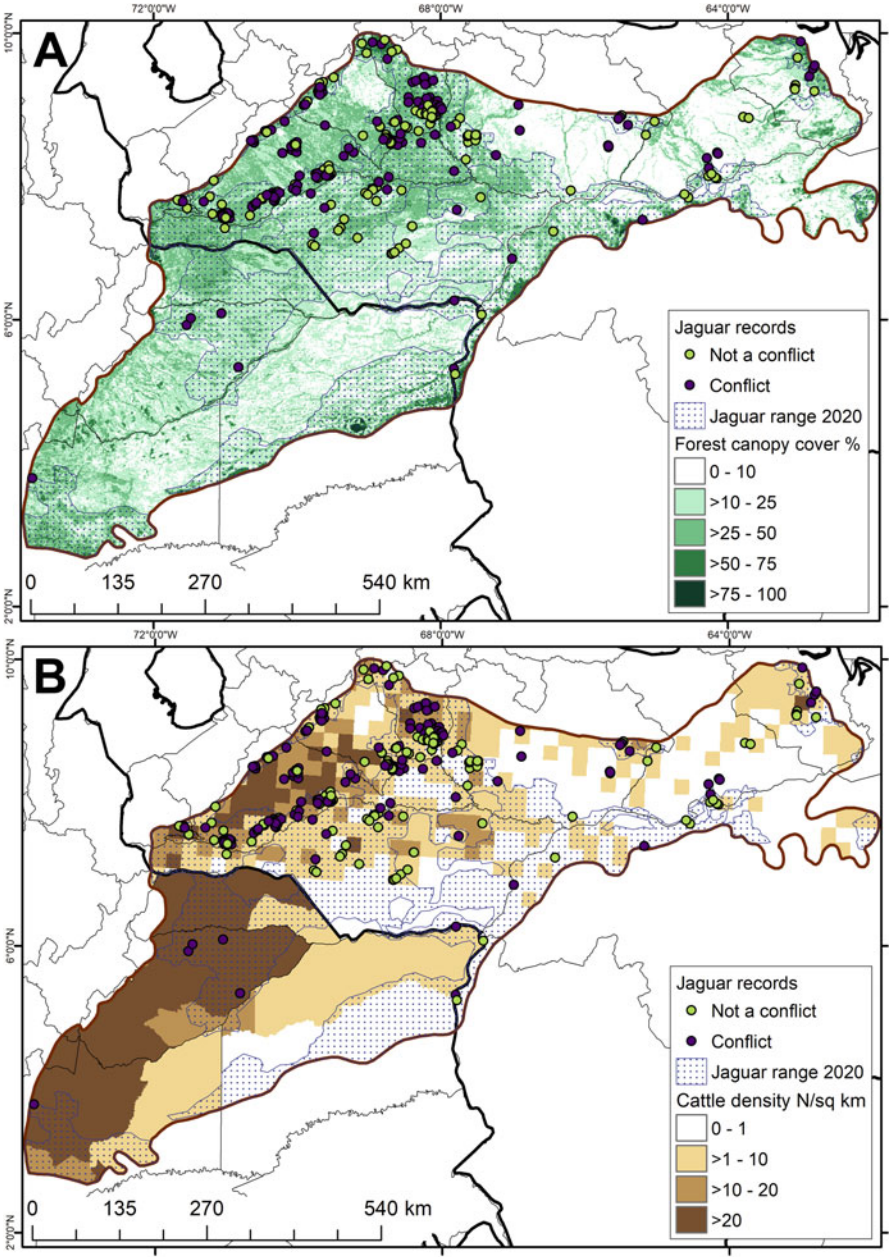

Fig. 9.24 Human–jaguar conflict and nonconflict records compared to: (**a**) distribution of forest canopy cover, (**b**) distribution of cattle densities in the Llanos. Our data on human–jaguar conflicts are mostly limited to the Venezuelan part of the Llanos, because few interviews were conducted in the Colombian Llanos

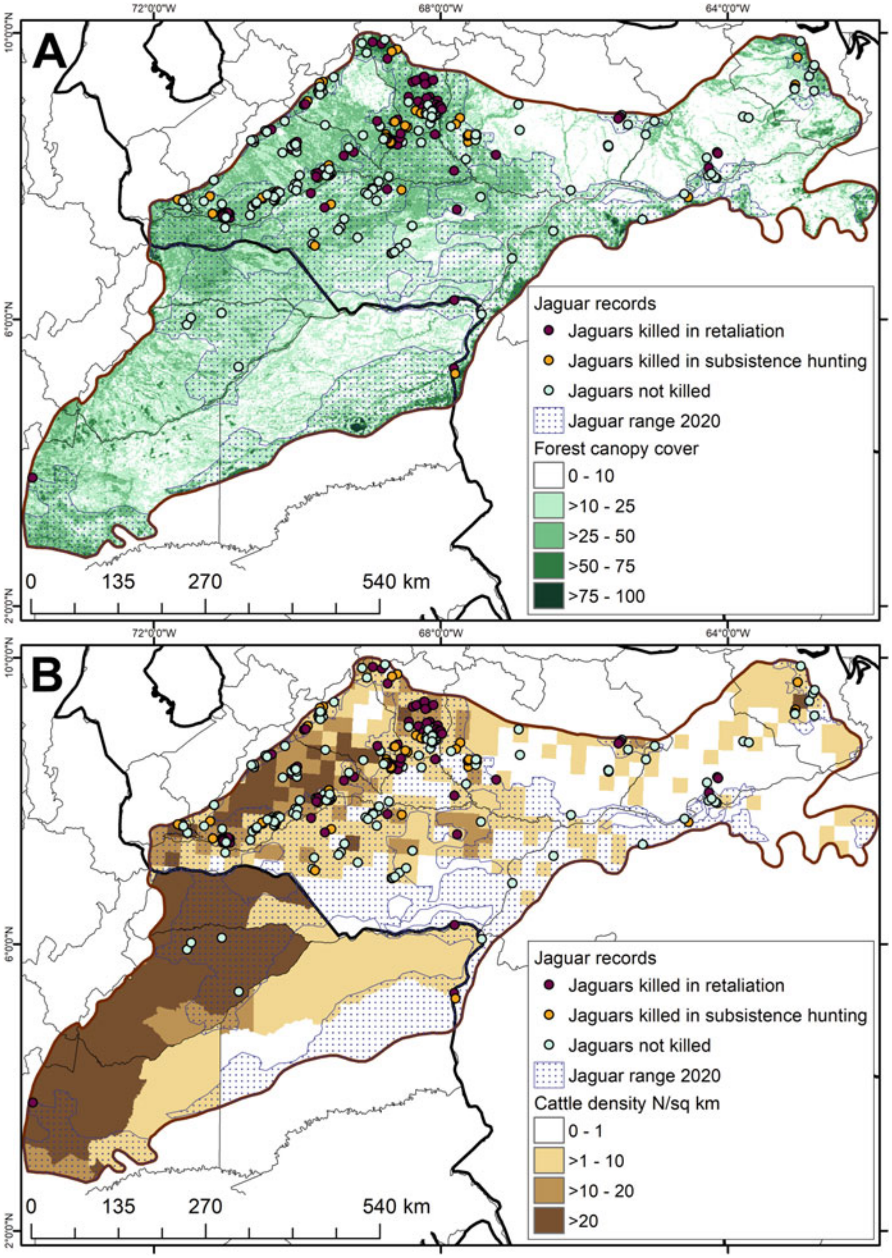

Fig. 9.25 Records of live jaguars and jaguars killed in retaliation and in subsistence hunting compared to: (**a**) distribution of forest canopy cover, (**b**) distribution of cattle densities in the Llanos (N/km^2). Our data on jaguar mortality are mostly limited to the Venezuelan part of the Llanos, because few interviews were conducted in the Colombian Llanos

Table 9.4 Number and percentage of conflict and nonconflict jaguar records, split to records of live and killed jaguars, collected within areas with different forest canopy cover in the Llanos; compare Figs. 9.24 and 9.25

		Conflict			Nonconflict			
Forest canopy cover (%)	Area thousands km^2 (%)[a]	Jaguars not killed N (%)	Jaguars killed in retaliation N (%)[b]	Total N (%)[a]	Jaguars not killed N (%)	Jaguars killed in subsistence hunting N (%)[b]	Total N (%)	Total records N (%)
0–10	35.6 (17)	2 (2)	3 (4)	5 (3)	2 (2)	1 (2)	3 (2)	8 (2)
10–25	86.6 (40)	9 (11)	18 (23)	27 (17)	29 (23)	7 (17)	36 (22)	63 (19)
25–50	80.0 (37)	63 (77)	47 (60)	110 (69)	69 (56)	31 (74)	100 (60)	210 (64)
50–100	12.2 (6)	8 (10)	10 (13)	18 (11)	24 (19)	3 (7)	27 (16)	45 (14)
Total	214.4	82 (100)	78 (100)	160 (100)	124 (100)	42 (100)	166 (100)	326 (100)

[a]Chi-squared test for comparisons of the frequency distribution of total conflict records with the percentage distribution of area with given forest canopy cover: chi^2 = 56.6, $p < 0.001$, [b]chi-squared tests for comparisons of percentage distributions of retaliatory killing and subsistence hunting records: chi^2 = 8.6, $p = 0.035$

Table 9.5 Conflict and nonconflict jaguar records, split to records of live and killed jaguars, collected in areas with different cattle densities in the Llanos; compare Figs. 9.24 and 9.25

		Conflicts			Nonconflicts			
Cattle Density N/km^2	Area thousands km^2 (%)^a	Jaguars not killed N (%)	Jaguars killed in retaliation N (%)^b	Total conflicts N (%)^a	Jaguars not killed N (%)	Jaguars killed in subsistence hunting N (%)^b	Total nonconflicts N (%)	Total records N (%)
0–1	83.6 (39)	13 (16)	7 (9)	20 (12)	22 (18)	7 (17)	29 (17)	49 (15)
>1–10	70.8 (33)	33 (40)	42 (54)	75 (47)	53 (43)	30 (71)	83 (50)	158 (48)
>10–20	23.6 (11)	26 (32)	23 (29)	49 (31)	44 (35)	4 (10)	48 (29)	97 (30)
>20–1	36.5 (17)	10 (12)	6 (8)	16(10)	5 (4)	1 (2)	6 (4)	22 (7)
Total	(100)	82 (100)	78 (100)	160 (100)	124 (100)	42 (100)	166 (100)	326 (100)

[a] Chi-squared test for comparisons of the frequency distribution of total conflict jaguar records with the percentage distribution of area with given cattle density: $\mathrm{chi}^2 = 61.6$, $p < 0.001$, [b] chi-squared tests for comparisons of distributions of retaliatory killing and subsistence hunting records $\mathrm{chi}^2 = 29.4$, $p < 0.001$

In the Llanos, jaguars are closely associated with aquatic habitats, and a large proportion of their prey is associated with water (Scognamillo et al. 2003). Our results are consistent with these features of jaguar biology. In the logistic regression model, three variables related to water (normalized difference water index – NDWI, occurrence of water bodies and flooded habitats, and amount of precipitation) had important positive impacts on jaguar occurrence. Other three variables also had positive impacts: gross primary productivity (GPP) that, as other vegetation indices, is related to prey abundance (Pettorelli et al. 2011; Pettorelli 2013; Jędrzejewski et al. 2018), forest cover, and legal area protection. Forests are an important jaguar habitat across its range (De Angelo et al. 2013; Jędrzejewski et al. 2018) and another source of important jaguar food (Foster et al. 2010). Protected areas prevent habitat transformation and reduce the impacts of illegal hunting (Naughton-Treves et al. 2005; Sollmann et al. 2008; Jędrzejewski et al. 2017a). The importance of protected areas and particularly of their size for jaguar occurrence in the Llanos was also indicated by other studies (Woodroffe and Ginsberg 1998; Payan et al. 2013). The human footprint index and road density had negative impacts on jaguar occurrence. Higher values of the human footprint index and higher road densities are related to higher human presence, higher impact of hunting, more intense land use, and habitat transformations (Sanderson et al. 2002b; Ibisch et al. 2016; Espinosa et al. 2018). Low road accessibility and low human density were identified as key decisive factors for jaguar occurrence in the Colombian Llanos (Payan et al. 2013). Our models also indicate that mean temperature, amount of agriculture, and cattle densities have nonlinear effects on jaguar occurrence, with a positive effect at some range of their values. Low cattle density may have a positive effect by being an additional prey resource for jaguars while it is not yet destructive for jaguar habitats; however, when mean cattle density is high in an area, jaguars disappear (Jędrzejewski et al. 2017b). Similarly, a small addition of agriculture may increase diversity and total biomass of prey (Devlin et al. 2023), but any larger land transformations to croplands have very destructive effects. This analysis confirms that the natural conditions on the Llanos were very favorable for jaguars, while anthropogenic changes, especially deforestation and the expansion of cattle farming and intensive agriculture, lead to the impoverishment of the environment and the decline of the jaguar population.

Due to the environmental changes that already occurred, jaguar habitats and populations have become significantly fragmented, with vast areas that are no longer suitable for this carnivore. However, individual jaguars often disperse, e.g., along the rivers, from jaguar-inhabited areas to anthropogenic areas, where they often get killed. On the other hand, in several cattle ranches or around human settlements inside the jaguar range, jaguars may get extirpated due to deforestation or hunting, resulting in local absences, which we evidenced by interviews. This complex situation and spatially mixed coexistence of presence and absence points cause difficulties in modeling jaguar occurrence and estimating its range and population size in the Llanos. We used a general framework of hierarchical modeling and combined different types of models to improve our assessment of the jaguar population in the Llanos.

Combining logistic regression with kriging interpolation gave better estimates of jaguar distribution than when using any of these methods alone. The IUCN guidelines for estimating species distributions for Red List assessments recommend deriving species distributions from direct mapping of species records (IUCN Red List Technical Working Group 2019), a similar method to the kriging interpolation that we used. However, such methods give good results only where dense presence–absence data are available and cannot be applied to the areas where there is no data. The species distribution models using logistic regression may also provide reliable information about areas for which data are missing, but the results are also highly dependent on the quantity and quality of presence–absence data and the selection and quality of predicting variables (Hirzel et al. 2006). In our analysis, predictions based on the logistic regression alone overestimated jaguar distribution in several parts of the Llanos, for example along the large rivers where habitats may be suitable, but they are fragmented or surrounded by strongly transformed areas. The combination of both methods largely eliminates the shortcomings of each one.

In a similar way, we combined the density model with the occurrence model to improve the estimate of the jaguar population in the Llanos. Jaguar densities and home range sizes are strongly shaped by environmental productivity factors, and this relationship allows modeling and predicting the potential jaguar population density at a large geographic scale (Jędrzejewski et al. 2018; Thompson et al. 2021). In the Llanos, jaguar populations may reach quite high densities (over 4 adult jaguars/100 km^2) compared to other ecoregions (Jędrzejewski et al. 2017c). However, various human impacts, especially human-caused mortality, leave some jaguar territories uninhabited, lowering the effective population size and density (Boron et al. 2016). The probabilities of occurrence predicted by distribution models that incorporate various anthropogenic factors can be interpreted as an indicator of territory occupancy and can be used to adjust the densities predicted by density models (Jędrzejewski et al. 2018). Using this approach gives more reliable estimates of population estimates than using field density estimates or density models alone. Since most field estimates of the population density of large carnivores are carried out in well-preserved environments, often in protected areas, and are additionally burdened with various methodological errors such as too small study areas or too short sampling periods, it is necessary to correct density predictions accordingly when estimating population sizes of large carnivores (Tobler and Powell 2013; Jędrzejewski et al. 2017c, 2018; Murphy et al. 2022).

Jaguar attacks on cattle and retaliatory killings of jaguars are frequent and widespread all over the Llanos, as documented by our analysis and by other authors (Hoogestein et al. 1993, 2002; González Fernández 1995; Payan et al. 2013; Jędrzejewski et al. 2014). Retaliatory killing and deforestation are the main drivers of jaguar local extinctions and range decrease (Jędrzejewski et al. 2017b). We found that conditions that predispose a given area to conflict and retaliatory killing of jaguars are a moderate density of cattle coexisting with a higher forest cover. Our results may help identify areas where conflicts are most likely. Additionally, jaguars are also hunted by subsistence hunters, which are numerous in the area. Overlapping retaliatory and subsistence hunting may cause still faster jaguar declines but also may exert detrimental effects on the activity patterns and other unique behaviors of jaguars discovered in the Llanos (Jędrzejewski et al. 2017b, c, 2021, 2022; Stasiukynas et al. 2021).

The Llanos is an important jaguar habitat and still today it is inhabited by over 3000 individuals. However, the jaguar range and likely also its numbers are quickly declining. Urgent conservation actions are needed to stop this decline. One of the most important is increasing the number and extension of protected areas. Currently, with 14% of the jaguar range protected, the Llanos ecoregion has one of the worst situations in the entire jaguar range. For comparison, 28% of the area of the huge Amazon ecoregion is covered by protected areas and an additional 27% by indigenous territories, which also play an important role in conservation (RAISG 2020). The second major need is to stop habitat transformation, especially deforestation. Better management of human–jaguar conflicts is also an important task. Education programs directed to promote the wider application of antidepredation technics by cattle ranchers may decrease the rate of conflicts and help in jaguar conservation (Hoogesteijn and Hoogesteijn 2010, 2011; Castaño Uribe et al. 2016).

Besides jaguars, the Llanos is an ecoregion of high biodiversity and should be protected also for this reason. Jaguars are good indicators of the state of conservation of any area: they are present when natural conditions prevail and they decline when habitats are strongly changed by human impacts, as our analyses have shown. Thus, any actions taken to protect jaguars will help to protect several other species (Thornton et al. 2016).

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Supplementary Material

Table 9.6 Information on candidate predictive variables used in the spatial analysis

No	Variable name, units, and expected impact on jaguar occurrence: [+] – positive, [−] – negative	Data description/time period to which the data refer/Notes and source	Reference #
1	Mean annual temperature (°C) [+] or [−]	The original value downloaded from the WorldClim webpage was divided by 10 to express it in Centi-grades. Mean from 1950 to 2000; Bioclim WorldClim - Global Climate Data. www.worldclim.org/bioclim	Hijmans et al. (2005)
2	Annual precipitation (mm) [+]	In the tropics precipitation values are usually related to productivity. Mean from 1950 to 2000; Bioclim WorldClim - Global Climate Data. www.worldclim.org/bioclim	Hijmans et al. (2005)
3	CANOPY Mean forest canopy cover (%) [+]	% forest cover calculated for a square kilometre. Mean for 2018; MODIS: MOD44B. https://lpdaac.usgs.gov/	Hansen et al. (2003), DiMiceli et al. (2011)
4	NPP_{MEAN} Mean net primary productivity (grams of elemental carbon per m^2) [+]	The net (without respiration) amount of solar energy converted to plant organic matter through photosynthesis, a measure obtained from satellite imagines. Mean from 1981 to 2014; MODIS: MOD17A3. http://www.ntsg.umt.edu/project/mod17	Zhao et al. (2005)
5	NPP_{SD} Standard deviation of net primary productivity [+] or [−]	A measure of seasonality in primary productivity or seasonal abundance of plant organic matter. Mean from 1981 to 2014; MODIS: MOD17A3. http://www.ntsg.umt.edu/project/mod17	Zhao et al. (2005)
6	GPP_{MEAN} Mean gross primary productivity (grams of elemental carbon per m^2) [+]	Total amount of chemical energy produced by plants through photosynthesis. Mean from 1981 to 2014; MODIS: MOD17A3. http://www.ntsg.umt.edu/project/mod1	Zhao et al. (2005)
7	GPP_{SD} Standard deviation of gross primary productivity [+] or [−]	A measure of seasonality in primary productivity or seasonal abundance of plant organic matter. Mean from 1981 to 2014; MODIS: MOD17A3. http://www.ntsg.umt.edu/project/mod17	Zhao et al. (2005)

(continued)

Table 9.6 (continued)

No	Variable name, units, and expected impact on jaguar occurrence: [+] – positive, [−] – negative	Data description/time period to which the data refer/Notes and source	Reference #
8	$\mathrm{NDVI}_{\mathrm{MEAN}}$ Mean Normalized Difference Vegetation Index [+]	Vegetation index obtained from satellite imagines, measuring photosynthetic activity of plants and indicating vegetation productivity and abundance. NDVI quantifies amount of green vegetation by measuring the difference between near-infrared (which vegetation strongly reflects) and red light (which vegetation absorbs). Mean from 1981 to 2014; MODIS: MCD43A4_NDVI. https://lpdaac.usgs.gov/	Pettorelli et al. (2005, 2011)
9	$\mathrm{NDVI}_{\mathrm{SD}}$ Standard deviation of normalized difference vegetation index [+] or [−]	Measure of seasonality or seasonal abundance of vegetation Mean from 1981 to 2014; MODIS:MCD43A4_NDVI. https://lpdaac.usgs.gov/	Pettorelli et al. (2005, 2011)
10	$\mathrm{EVI}_{\mathrm{MEAN}}$ Enhanced vegetation index [+]	Vegetation abundance and productivity measure. Similar to NDVI, with higher sensitivity and accounting for differences between canopy and background. Mean from 1981 to 2014; MODIS:MCD43A4_EVI. https://lpdaac.usgs.gov/	Huete et al. (2002, 2006), Jiang et al. (2008)
11	$\mathrm{EVI}_{\mathrm{SD}}$ Standard deviation of Enhanced Vegetation Index [+] or [−]	Measure of seasonality or seasonal abundance of vegetation. Mean from 1981 to 2014; MODIS: MCD43A4_EVI. https://lpdaac.usgs.gov/	Huete et al. (2002, 2006), Jiang et al. (2008)
12	$\mathrm{NDWI}_{\mathrm{MEAN}}$ Mean annual value of normalized difference water index (values -1 to 1) [+]	Measure of water content in vegetation (leaves), often used to detect droughts; however, it indicates also ground water content; positive values are typically very moist or flooded areas; while negative values are drier areas (i.e. terrestrial vegetation and bare soil). Mean from 1981 to 2014; MODIS:MCD43A4_NDWI. https://lpdaac.usgs.gov/	Gao (1996)
13	$\mathrm{NDWI}_{\mathrm{SD}}$ Standard deviation of normalized difference water index [+] or [−]	Variability/seasonality in water content in vegetation; high values indicate seasonal flooding or seasonal changes between fresh vegetation and droughts. Mean from 1981 to 2014; MODIS: MCD43A4_NDWI. https://lpdaac.usgs.gov/	Gao (1996)

(continued)

Table 9.6 (continued)

No	Variable name, units, and expected impact on jaguar occurrence: [+] – positive, [−] – negative	Data description/time period to which the data refer/Notes and source	Reference #
14	Human population density people/km^2. logarithmically transformed [−]	Mean for 2011; http://sedac.ciesin.columbia.edu/data	Balk et al. (2006)
15	Human Footprint Index 2004. (values 0 to 100) [-]	Index reflecting human caused environmental changes based on data from 1995 to 2004; NASA Socioeconomic Data and Applications Center (SEDAC). http://sedac.ciesin.columbia.edu/data	Sanderson et al. (2002a, b), Venter et al. (2016a, b)
16	Human Footprint Index – 2009 (values 0 to 50) [-]	Index approximating a change in human foot print between 1993 and 2009; NASA Socioeconomic Data and Applications Center (SEDAC). http://sedac.ciesin.columbia.edu/data	Sanderson et al. (2002a, b), Venter et al. (2016a, b)
17	Protected Areas Protection status: if inside a protected area – value 1, if outside – value 0 [+]	All categories of protected areas included except forestry reserves; World map of protected areas (WDPA - data for 2015). http://www.protectedplanet.net/ Amazonia Socioambiental RAISG 2019. https://www.amazoniasocioambiental.org/es/mapas/#!/areas	IUCN & UNEP-WCMC (2016)
18	Indigenous territories: if inside – value 1, if outside – value 0 [+]	We included indigenous territories as they have important role in jaguar conservation; Amazonia Socioambiental RAISG 2019. https://www.amazoniasocioambiental.org/es/mapas/%22%20/l%20%22!/areas Data verified for each country with webpages of respective ministries of environment.	IUCN & UNEP-WCMC (2016)
19	Road density index derived from GRIP4_Global Roads (values 0 to 4) [−]	An index approximating road density. The four main road categories were converted to raster and then summed at each 1 km^2 pixel. From this value we calculated a moving average within a distance of 20 km on both sides of the road (using Focal statistic/mean function in ArcGis). Data for 2018; GRIP4_GlobalRoads. https://www.globio.info/download-grip-dataset	Meijer et al. (2018)

(continued)

Table 9.6 (continued)

No	Variable name, units, and expected impact on jaguar occurrence: [+] – positive, [−] – negative	Data description/time period to which the data refer/Notes and source	Reference #
20	Agriculture % Proportion of cropland area in a 1 km^2 cell [+] or [−]	Calculated from the Land Cover data at 300 m resolution Data for 2010 – used for model construction; https://maps.elie.ucl.ac.be/CCI/viewer/download.php	Cover (2017)
21	Pasture % Proportion of pasture area in a 1 km^2 cell [+] or [−]	Calculated from the Land Cover data at 300 m resolution Data for 2010 – used for model construction; https://maps.elie.ucl.ac.be/CCI/viewer/download.php	Cover (2017)
22	Water bodies and flooded areas (%) Proportion of area in a 1 km^2 cell [+]	Calculated from the Land Cover data at 300 m resolution Data for 2010 – used for model construction; https://maps.elie.ucl.ac.be/CCI/viewer/download.php	Cover (2017)
23	Cattle density [+] or [−]	Cattle density N/km^2. Data for 2016; Data obtained from the respective ministries of agriculture of Colombia and Venezuela: 1) Instituto Colombiano Agropecuario – ICA, Bogotá – Colombia https://www.ica.gov.co/getdoc/8232c0e5-be97-42bd-b07b-9cdbfb07fcac/Censos-2012.aspx 2) Censo Agropecuario Nacional 2016; Dirección General de Ganadería de Especies Mayores. Ministerio de Agricultura y Tierras, Venezuela	

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Chapter 10
Using Camera-Trap Data to Simultaneously Estimate Jaguar (*Panthera onca*) Density and Resource Selection in the Paraguayan Dry Chaco

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Abstract Habitat loss and human-caused mortality have led to an approximate 50% reduction of the distribution of the jaguar (*Panthera onca*). The large contraction in the jaguar's occurrence points to a need to understand its population size and habitat preferences to apply to the species' conservation. Typically, jaguar densities are estimated with capture–recapture modeling of photographic captures of individually identifiable individuals, while habitat selection is estimated from telemetry data. However, advances in spatial capture-recapture modeling now permit the simultaneous estimation of density and habitat selection based solely upon photographic detection data from camera-trapping grids. Here, we used data from 356 double camera-trap stations across five sites in the Paraguayan Dry Chaco to simultaneously estimate jaguar density and resource selection. We found that jaguar densities ranged from 0.58 to 1.39 individuals/100 km^2. At the spatial scale of our analysis, jaguars showed a strong preference for forest cover, while space use was not affected by the Human Footprint Index. Our density estimates were consistent with previous estimates based upon a subset of our data, as well as with estimates for jaguar populations in other dryland ecosystems. Furthermore, the strong selection for forest was also consistent with range-wide patterns in jaguar space use and habitat selection derived from telemetry data. Due to extensive and ongoing deforestation in the Dry

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Chaco, combined with high human-caused mortality, the jaguar is critically endangered in Paraguay. Although we show that jaguars can persist in anthropogenically altered landscapes in Paraguay, their long-term survival at the national level is strongly dependent upon the effective enforcement of the national jaguar conservation law, and application of the national jaguar management plan, to mitigate negative population effects from habitat loss and human-caused mortality.

Keywords Dry Chaco · Jaguar · Medanos · Paraguay · Resource selection · Spatial capture-recapture

10.1 Introduction

Apex predators are often used as conservation surrogates as they may play important roles in affecting ecosystem function and serve as bioindicators (Sergio et al. 2008). In the Neotropics, the occurrence of the jaguar (*Panthera onca*), the largest felid in the Americas, is associated with high levels of biodiversity, the provision of multiple ecosystem services, and consequently serves as an indicator of the conservation value of landscapes (Thornton et al. 2016; Burke et al. 2019). Since the jaguar is a forest-associated species throughout its range and across ecosystems types, and is sensitive to landscape-scale anthropogenic factors (Morato et al. 2018; Alvarenga et al. 2021; Thompson et al. 2021), it is a logical species to be used to examine the ecological effects of forest loss and other landscape-scale anthropogenic factors. However, the jaguar's distribution has been reduced by about 50% range-wide and by 80% outside of Amazonia due to habitat loss and human–jaguar conflict driven persecution (de la Torre et al. 2018). This reduction in distribution indicates an important need to understand the effects of habitat loss and degradation on jaguar populations, the implications for their conservation, and in turn the ecosystem services with which they are associated.

Within the jaguar's distribution, habitat conversion from expanding agricultural production has been acute during the last 20 years in dry forest and savanna systems in southern South America, particularly in the Dry Chaco of Argentina, Bolivia, and Paraguay which has undergone some of the highest rates of forest loss in the world (Curtis et al. 2018; Zalles et al. 2021; Da Ponte et al. 2021; Buchadas et al. 2022). Despite its high levels of habitat loss and often high levels of biodiversity, the Dry Chaco receives relatively little attention from the global conservation community due to a strong focus upon tropical humid systems (Redford et al. 1990; Kuemmerle et al. 2017; Qin et al. 2022). This pattern was discussed by Redford et al. (1990) who, in referring to the Dry Chaco, pointed out that "the attention to rainforest has acted like blinders" and "The concentration on rainforests, and the rhetoric that accompanies it, has led to the neglect of other severely threatened ecosystems."

The statements of Redford et al. (1990) were prescient as they foresaw the forthcoming deforestation in the Dry Chaco and its implications for conservation that were to occur during the twenty-first century. However, in recent years, there has been an increasing amount of research on the effects of deforestation on multiple

Fig. 10.1 Camera-trap record of Jaguar (*Panthera onca*) in the Paraguayan Medanos

taxa and communities in the Dry Chaco (Periago et al. 2014; Cartes et al. 2015; Núñez-Regueiro et al. 2015; Semper-Pascual et al. 2018, 2020; Camino et al. 2020, 2022; de la Sancha et al. 2021), including the jaguar (Fig. 10.1) (Altrichter et al. 2006; Noss et al. 2012; Quiroga et al. 2014; Thompson and Velilla 2017; McBride and Thompson 2018; Romero-Muñoz et al. 2019; Thompson et al. 2020, 2021, 2022). Importantly, for the jaguar, although forest availability is key, it is not the sole factor determining jaguar occurrence in the Dry Chaco. Anthropogenic factors have a disproportionately strong negative influence on jaguar occurrence despite sufficient habitat and prey availability (Quiroga et al. 2014; McBride and Thompson 2018; Romero-Muñoz et al. 2019, 2020; Thompson et al. 2020). Consequently, evaluating the relative importance of both environmental and anthropogenic factors on jaguar density and habitat use is a necessary precursor to understand how deforestation in the Dry Chaco is affecting the jaguar population.

Advances in spatial capture–recapture (SCR) modeling allow for the simultaneous estimation of density, habitat selection, and connectivity (Royle et al. 2013b; Sutherland et al. 2015; Morin et al. 2017), providing a powerful framework to integrate population and landscape ecology (Royle et al. 2018). We previously took advantage of this framework and found that jaguar density and landscape connectivity in the Paraguayan Dry Chaco were negatively affected by increases in deforestation within landscapes (Thompson et al. 2022), which was consistent with expectations based upon patterns in jaguar space use (Thompson et al. 2021). Furthermore, we illustrated the importance and value of accounting for potential bias stemming from habitat-driven space use by jaguars when estimating density in a spatial capture–recapture modeling framework (Thompson et al. 2022).

Historically, the movements of animals within their home range (third-order habitat selection; Johnson 1980), and the drivers of those movements (Manly et al. 2002), have typically been estimated using telemetry data. However, SCR modeling has been extended to estimate resource selection by taking advantage of the spatial information provided by spatial recaptures of individuals (Royle et al. 2013b;

Sollmann et al. 2016; Linden et al. 2018). This advance consequently allows for the estimation of habitat use within activity areas using Resource Selection Functions (RSF; Manly et al. 2002) based solely upon spatial capture-recapture data, while allowing to simultaneously estimate density (Royle et al. 2013b).

We took advantage of the capabilities of SCR modeling to include RSFs to simultaneously estimate habitat selection within activity areas and density of jaguars in the Paraguayan Dry Chaco. This allowed us to explore how jaguar space use was affected by forest availability and landscape-scale anthropogenic factors across landscapes with differing intensities of forest conversion. Our sampling areas included landscapes with varying levels of deforestation, as well as the Medanos, a mixed matorral – savanna – forest system within the Bolivian–Paraguayan Dry Chaco, where in Paraguay jaguars have yet to be studied. Recognizing that jaguars demonstrate a general preference for forest cover, avoidance of pastures, reduced occurrence in response to anthropogenic factors, and in the Paraguayan Dry Chaco reduced densities in relation to deforestation (Morato et al. 2018; Thompson et al. 2020, 2021, 2022; Alvarenga et al. 2021), we expected that (1) within their activity areas, jaguars will select forest regardless if the heterogeneity in forest availability was natural or due to deforestation, while (2) areas with higher anthropogenic impacts will be avoided. Furthermore, we intended to show the capabilities of SCR modeling to expand its utility beyond density estimation to address key conservation questions, such as resource selection, solely from camera-trap-based capture–recapture data.

10.2 Methods

10.2.1 Study Site

The Dry Chaco extends across ~787,000 km^2 in parts of Argentina (62%), Paraguay (22%), and Bolivia (16%) and is the largest subtropical dry forest system in the world (Olson et al. 2001). The Dry Chaco is a global deforestation hotspot, whereby ranching and row crop agriculture have driven the deforestation of about 27% of the ecoregion's forest (Caldas et al. 2015; Da Ponte et al. 2021; Hansen et al. 2013; Vallejos et al. 2015). In Paraguay, 64,000–77,000 km^2 (~45%) of its Dry Chaco forest area was lost by 2020, mostly due to pasture creation for cattle raising, equating to an annual forest transformation rate of about 4% or ~ 500 ha/day/year since 2000 (Fig. 10.2; Hansen et al. 2013; Caldas et al. 2015; Vallejos et al. 2015; Baumann et al. 2017; Da Ponte et al. 2021). Importantly, from a conservation perspective, the forest loss during the past two decades has occurred in wilderness areas of high conservation value, so that since 2000 the area of intact forest landscapes in the Paraguayan Dry Chaco has decreased by 76% (Watson et al. 2018; Williams et al. 2020).

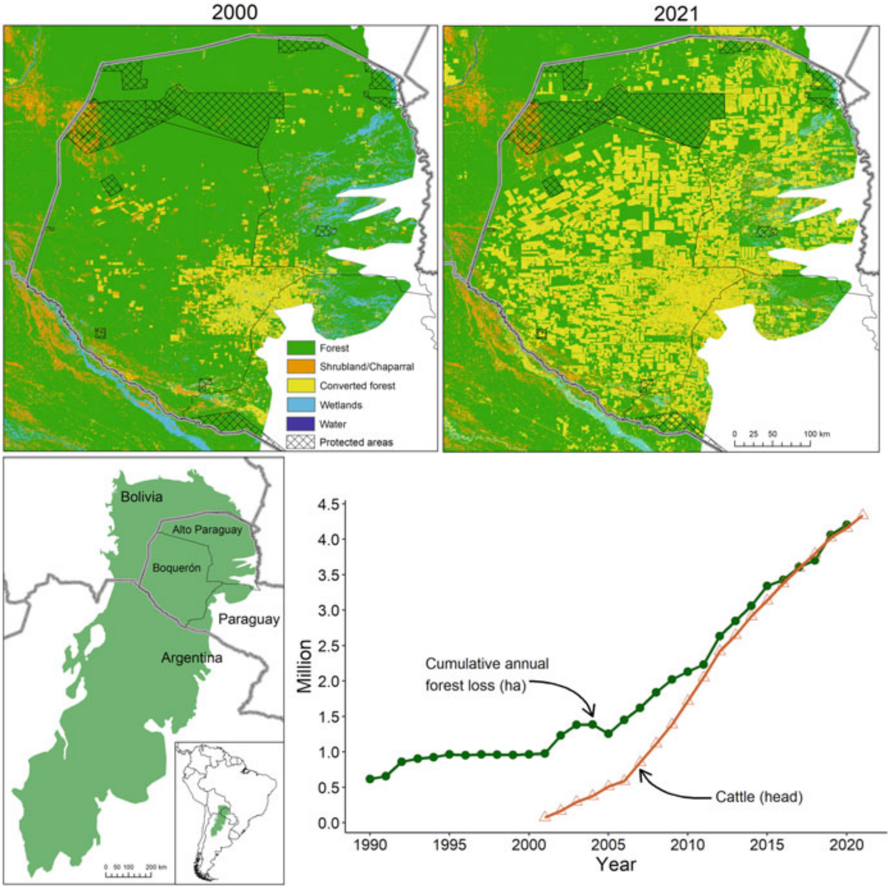

Fig. 10.2 Location of the Dry Chaco within South America and land cover and protected areas in the Paraguayan Dry Chaco for the years 2000 and 2021. The graph shows the cumulative annual forest loss and cattle population from 1990 to 2021 for the Paraguayan departments of Alto Paraguay and Boquerón, which encompass the large majority of the Dry Chaco in Paraguay. (Data from: https://www.senacsa.gov.py/index.php/informacion-publica/estadistica-pecuaria)

10.2.2 Camera-Trap Sampling

During the austral fall to winter (May–September) 2016–2018, we employed camera-trap sampling at four sites with semideciduous xeric forest in the Dry Chaco (Mereles 2005; Mereles et al. 2019) along a gradient of deforestation intensity ranging from 17% to 51% deforested. We employed 335 double camera-trap stations located on roads, firebreaks, or along fence lines (Fig. 10.3, Table 10.1; Thompson et al. 2022). Additionally, during 2018 we also sampled a site in the Medanos within the Dry Chaco, a matorral – savanna system interspersed with xeric forest (Mereles 2005; Mereles et al. 2019) which previously had not been sampled for jaguars in Paraguay (Fig. 10.3, Table 10.1). The initial four sampling sites were all located on

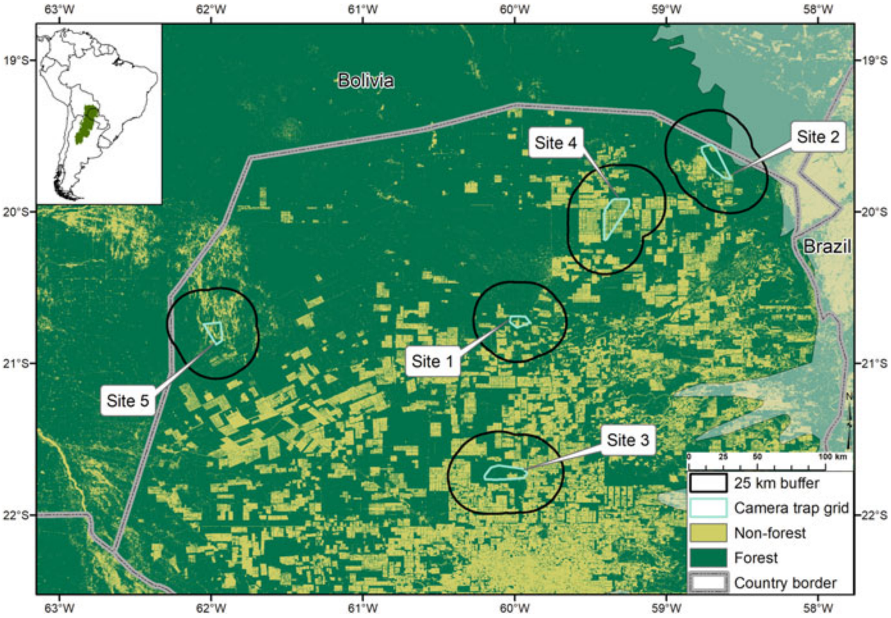

Fig. 10.3 Locations of camera-trap grids and their 25 km buffers in the Paraguayan Dry Chaco (Olson et al. 2001) in relation to forest cover in 2017 (Hansen et al. 2013). Shaded areas are outside the limit of the Dry Chaco. Inset shows the location of the Dry Chaco within South America

private ranchlands and the site in the Medanos was on a private protected area and adjoining indigenous land.

Sampling periods ranged from 98 to 279 days, with a mean of 100 operational days per station per site (Table 10.1). The site with the longest sampling period (Site 4) resulted from its sampling grid being divided into two temporally overlapping sections (48 and 27 stations). The long sampling periods were justifiable to increase detections (Dupont et al. 2019; Tobler and Powell 2013), while we see no reason to expect any effect on density as a function of sampling year as there were no abnormal differences in temperature or precipitation among the 2016–2018 sampling periods (www.meteorologia.gov.py). Moreover, in our analysis we accounted for potential site-specific differences in detectability and space use (see Data analysis).

Minimum convex polygons of our trapping grids ranged between 80 and 282 km^2 and, as discussed by Thompson et al. (2022), were sufficiently large related to jaguar activity areas to minimize bias in density estimates (Sollmann et al. 2011; Tobler and Powell 2013). We defined our modeling state space with a 25-km buffer around our trapping grids (see Data analysis), with our initial four sampling sites having a proportional area deforested ranging from 17% to 51% (Hansen et al. 2013). At the fifth site in the Medanos, the majority of unforested land was naturally occurring matorral with some deforested areas, so 18% of the modeled state space did not include forest (Fig. 10.3, Table 10.1).

Table 10.1 Site-specific sampling characteristics of camera-trap grids in the Paraguayan Dry Chaco, including sex-specific number of individuals captured and recaptured (*n*), count of total captures, and count of spatial recaptures per site

						Females				Males			
						Total captures		Spatial recaptures		Total captures		Spatial recaptures	
Site	% area in forest	Mean HFI[a]	Number of sampling stations	Trap days	Mean operational days/station	*n*	Count	*n*	Count	*n*	Count	*n*	Count
1	73	236	86	9712	113	4	39	3	31	8	152	7	85
2	83	60	62	4038	65	4	38	4	17	9	47	4	29
3	49	428	112	12,552	112	4	100	4	47	2	97	2	50
4	59	262	75	8554	114	5	18	4	14	4	71	4	24
5	82	169	21	2037	97	3	17	3	13	6	56	4	25

[a] *HFI* Human Footprint Index

10.2.3 Data Analysis

We used spatial capture-recapture modeling framework incorporating resource selection (hereafter SCR–RS) to explore the effect of forest cover and anthropogenic pressures on jaguar resource selection while simultaneously estimating jaguar densities (Royle et al. 2013b; Sollmann et al. 2016). The SCR–RS modeling framework accommodates resource selection models by incorporating the resource selection information spatially inherent in camera-trapping data. This permits the estimation of resource selection parameters while relaxing the assumption of symmetrical distance in the SCR detection function, allowing for space use to be a function of differential habitat preferences. Apart from being able to estimate third-order habitat use directly from camera-trap data, accounting for habitat-driven differences in space use reduces bias in detectability when estimating density (Royle et al. 2013b). We considered this important given the preferred use of the forest by jaguars (Alvarenga et al. 2021; Morato et al. 2018; Thompson et al. 2021), and previous modeling of a subset of our data which demonstrated the importance of accounting for asymmetrical space use when estimating jaguar density in fragmented Dry Chaco forest (Thompson et al. 2022).

Using the photographic captures from our sampling we developed individual daily encounter histories for jaguars by assigning jaguar photographs to each sampling station by date and individual. Jaguars were identified by their spot patterns and sexed by genitalia, with juveniles accompanied by their mother excluded from the data set. Using these spatial encounter histories, we estimated densities for each site in a multisite (multisession) model in R (R Core Team 2019) using the *oSCR* package (Sutherland et al. 2015) with a state space delimited by a 25-km buffer from traps at a resolution of 1 km. Although in previous modeling of a subset of our data a resolution of 2 km was used (Thompson et al. 2022), we found that estimates were sensitive to resolutions greater than 1 km, which we attribute to the fine-grain nature of habitat heterogeneity in the additional site from the Medanos. Since jaguars in the Paraguayan Dry Chaco can move more than 14 km per day on average (McBride and Thompson 2018; Thompson et al. 2021) a 1 km resolution is consistent with the scale of jaguar space use in our study areas.

As in Thompson et al. (2022), we used the mean proportional area of forest as a biologically relevant metric to characterize forest availability. We developed maps of forest occurrence from 1 arc-second spatial data on forest canopy density corresponding to the year of our sampling (Hansen et al. 2013), classifying all areas with a forest canopy density of ≥15% as forest (based upon ground truthing and our familiarity with the study system), and then deriving the mean proportional forest area for each grid cell of our 1 km resolution state space. To quantify anthropogenic influences within our state spaces we used the Human Footprint Index (HFI) (Sanderson et al. 2002; Venter et al. 2016; wcshumanfootprint.org), taking the average value at the 1 km resolution for the year corresponding to the beginning of sampling for each site.

We tested a set of models that evaluated the probability of space use as a function of the proportional forest area and the HFI, additively or separately. Models always included a site (session) effect on density, to meet closure assumptions, and on σ (scale parameter of decline in p with distance) and detection (p) to account for potential differences in space use and detection, respectively among sites. The scale parameter σ describes the rate that the probability of detection (p) decreases with distance from the estimated activity center of individuals, whereby p_0 is the baseline detection probability at an individual's activity center. We also evaluated the effect of sex on σ and p_0. Model selection was based on rankings of Akaike Information Criteria (AIC) weights (Burnham and Anderson 2002). Since AIC has a tendency to select models with uninformative parameters with no ecological effects that do not reduce AIC but increase model complexity (Burnham and Anderson 2002; Arnold 2010), we excluded models with uninformative parameters from the final model set (Arnold 2010). A parameter was considered uninformative when its significance level was <85% since the effect of such parameters is insufficient to warrant their inclusion in a model (Arnold 2010).

Similar to Sollmann et al. (2016), we used linear discriminant analysis (Manly and Alberto 2016) to evaluate how modeling state spaces differ in anthropogenic and environmental characteristics to potentially explain the difference in jaguar densities among sites. We examined differences in proportional forest area, HFI, estimated net primary productivity (Zhao et al. 2005), and estimated mean annual precipitation along with its coefficient of variation (Fick and Hijmans 2017), using the mean values at the 1 km resolution of the modeling state spaces. We evaluated correlations among covariates from the discriminant functions that explained at least 95% of the between-group variance. We considered a strong correlation between covariables where coefficients were ≥ 0.7 and a p-value <0.05. The linear discriminant analysis was undertaken in R using the *MASS* package (Venables and Ripley 2002).

10.3 Results

We detected between 6 and 13 individual jaguars per site. One GPS collared individual from site 3 was censored because it was killed after moving outside our sampling area. The total number of recaptures per site ranged from 73 to 197 and the total spatial recaptures per site ranged from 38 to 116 (Table 10.1). Of the models evaluated, three contained 100% of the model weights, with the model including the effect of forest cover on resource selection, and no sex effect on detection probability (p_0) or on the spatial scale factor (σ); being the highest ranked supported by 53% of model weights (Table 10.2). This model indicated a preference by jaguars for areas with increasing proportional forest cover ($\alpha = 1.31$, SE $= 0.2$; Table 10.3). The other two models included an uninformative parameter for the sex (-0.18, SE $= 0.21$) on detection probability (p_0) or HFI ($\alpha = 0.06$, SE $= 0.29$) on resource selection and consequently were excluded. Based upon the best supported model, density estimates ranged from 0.58 to 1.39 individuals/100 km^2 and fully forested areas were

Table 10.2 Top-ranking spatial capture–recapture models from the examined model set based upon the covariates used in the resource selection component of the capture–recapture model

Model	K	AIC	ΔAIC	weight
Forest cover	21	2543.87	0.00	0.53
Forest cover + sex	22	2545.15	1.28	0.28
Forest cover + HFI	22	2545.83	1.96	0.19

All models evaluated included the effect of site on density, detection, and σ (scale parameter of decline in detectability (p) with distance)

Table 10.3 Parameter estimates, standard errors (SE), and lower (95 L) and upper (95 U) 95% confidence intervals from the top ranked model

Parameter	Estimate	SE	95 L	95 U
p_0 (intercept)	−0.32	0.31	−0.93	0.29
p_0 (site 2)	−0.16	0.40	−0.94	0.62
p_0 (site 3)	−0.08	0.26	−0.59	0.43
p_0 (site 4)	−0.75	0.49	−1.71	0.21
p_0 (site 5)	−0.52	0.32	−1.15	0.11
σ (intercept)	8.50	0.12	8.26	8.74
σ (site 2)	−0.31	0.16	−0.62	0.00
σ (site 3)	−0.40	0.13	−0.65	−0.15
σ (site 4)	−0.11	0.15	−0.40	0.18
σ (site 5)	0.13	0.20	−0.26	0.52
α (forest cover)	1.31	0.20	0.91	1.69
D (intercept)	−4.50	0.36	−5.21	−3.79
D (site 2)	0.25	0.48	−0.69	1.19
D (site 3)	−0.55	0.55	−1.63	0.53
D (site 4)	−0.62	0.50	−1.60	0.36
D (site 5)	−0.58	0.55	−1.66	0.50
Ψ (site 1)	0.69	0.61	−0.51	1.89
Ψ (site 2)	0.81	0.60	−0.37	1.99
Ψ (site 3)	−0.69	0.87	−2.40	1.02
Ψ (site 4)	−0.22	0.67	−1.53	1.09
Ψ (site 5)	0.51	0.73	−0.92	1.94

D and σ are on the log scale and relate to density per grid cell and km, respectively. $p0$, α (Forest cover), and ψ, the baseline detectability probability, coefficient on space use for proportional forest cover, and probability of being a male, respectively, are on the logit scale

estimated to be used 3.7 times more than completely deforested areas (Fig. 10.4). Baseline detectability at the mean forest cover value from each site was estimated to be between 62% and 80% (Table 10.4). Estimates of σ ranged from 3.3 to 5.6 km and sex ratio estimates had high uncertainty, but the estimated probability of being a male varied from 33% to 67% across sites (Table 10.4).

The first two discriminant functions of the habitat analysis explained 98.19% of the between-group variance among the five state spaces. The first discriminant function of the habitat analysis explained 84.07% of the between-group variance

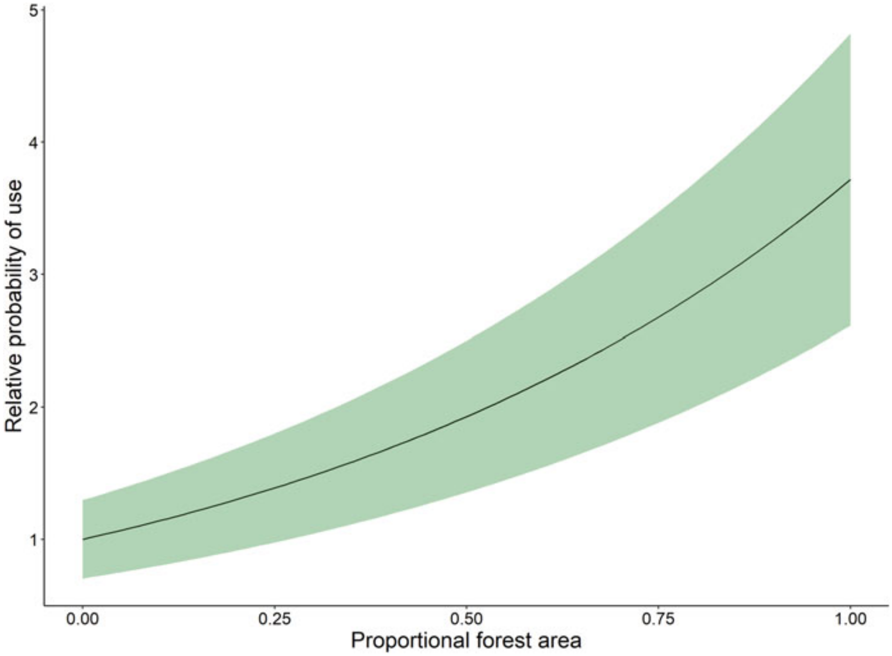

Fig. 10.4 Prediction of relative probability of site use by jaguars as a function of proportional forest area. Shaded area represents the 95% confidence interval

and was strongly negatively correlated with the coefficient of variance of annual precipitation and strongly positively correlated with mean annual precipitation (Table 10.5). The second discriminant function explained 14.12% of the variance between sites, with no strong correlations with covariates; however, net primary productivity showed a moderate correlation (Table 10.5). The effect of mean annual precipitation and its coefficient of variation grouped Sites 1–4 together, albeit with some among-site differences, while Site 5 from the Medanos was distinctly separated from the other sites (Fig. 10.5).

10.4 Discussion

By using the capacity of the SCR–RS model to estimate resource selection we further confirm the importance of forest cover for jaguars documented both range-wide (Morato et al. 2018; Thompson et al. 2021) and in the Dry Chaco (Romero-Muñoz et al. 2019; Thompson et al. 2022). We found strong third-order habitat selection for forested areas by jaguars in the Paraguayan Dry Chaco. Importantly, this relationship was evident in areas with forest fragmented through deforestation or naturally heterogeneous as in the matorral – savanna – forest system of the Medanos.

Table 10.4 Estimates and 95% confidence intervals (CI) from the best supported model for density, baseline detectability with the mean forest cover for each site ($p0$ (mean forest cover)), scale parameter (σ) by site, and sex ratio (expressed as the probability of an individual being a male

	Density (individuals/100 km^2)		Detectability ($p_{0(\text{mean forest cover})}$)		σ (km)		Sex ratio (probability of being a male)	
Site	Estimate	95% CI	estimate	95% CI	Estimate	95% CI	Estimate	95% CI
1	1.08	0.54–2.20	0.69	0.59–0.78	5.0	3.9–6.2	0.67	0.38–0.87
2	1.39	0.74–2.60	0.68	0.53–0.80	3.6	2.9–4.5	0.69	0.41–0.88
3	0.63	0.29–1.40	0.62	0.57–0.67	3.3	3.0–3.7	0.33	0.09–0.73
4	0.58	0.20–1.14	0.79	0.62–0.89	4.6	3.8–5.3	0.44	0.18–0.75
5	0.61	0.27–1.38	0.80	0.72–0.86	5.6	4.1–7.8	0.63	0.28–0.88

Table 10.5 Results of the functions of the linear discriminant analysis of landscape covariates for the five modeling state spaces in the Paraguayan Dry Chaco

	LD1	LD2	LD3	LD4
Landscape characteristic	*84.07*	*14.12*	*1.55*	*0.26*
Proportional forest area	−0.020 (0.008)	0.268 (<0.001)	0.038 (<0.001)	0.880 (<0.001)
Human footprint index	−0.068 (<0.001)	−0.387 (<0.001)	−0.201 (<0.001)	−0.702 (<0.001)
Net primary productivity	0.266 (<0.001)	0.649 (<0.001)	0.635 (<0.001)	−0.292 (<0.001)
Mean annual precipitation	0.974 (<0.001)	0.219 (<0.001)	−0.047 (<0.001)	−0.004 (<0.001)
Coefficient of variation mean annual precipitation	−0.943 (<0.001)	0.331 (<0.001)	−0.054 (<0.001)	0.002 (0.760)

Values in italics associated with the linear discriminant functions (LD) are the percentage of between-state space variance explained by each function, while column values are Pearson correlation coefficients and associated *p*-values (in parentheses) for the correlation of the discriminant function with each landscape covariate

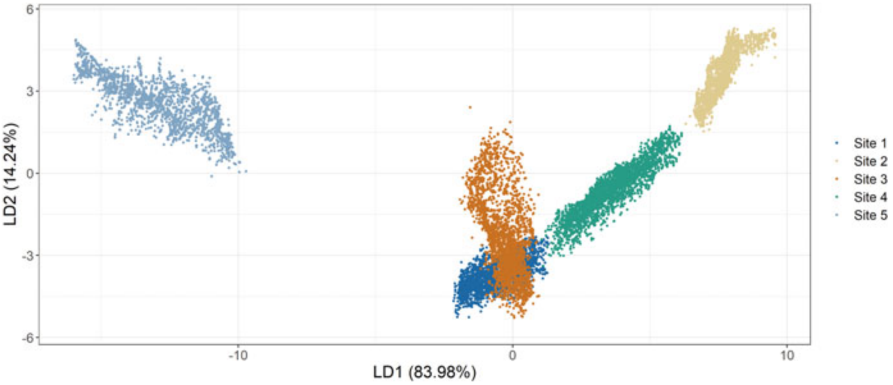

Fig. 10.5 Plot of the first and second linear discriminant functions for the habitat covariables from the spatial capture-recapture modeling state spaces. The first discriminant function was strongly negatively correlated with the coefficient of variation of annual precipitation and strongly positively correlated with mean annual precipitation. The second discriminant function only had a moderate positive correlation with net primary productivity

At the same time, we found no avoidance of anthropogenic factors represented by the HFI. Given the known negative relationship of anthropogenic factors on the occurrence and density of jaguars in the Dry Chaco (McBride and Thompson 2018; Romero-Muñoz et al. 2019; Thompson et al. 2020, 2022) this was unexpected and is likely due to the spatial scale of the HFI, or the information comprising the HFI, not capturing the relevant effects of jaguar space use.

Previously, in four of our five sites a negative relationship of deforestation on jaguar density was shown between the most and least deforested sites, as well as a strong negative effect of deforestation on population connectivity (Thompson et al.

2022). However, with the inclusion of the naturally heterogeneous site from the Medanos (Site 5), this relationship was not evident as its estimated density was similar to the most deforested of our sites (Sites 3 and 4). Nor did the linear discriminant analysis find a strong difference in net primary productivity among sites, which has been shown to decrease jaguar spatial needs, and in turn lead to increased density (Thompson et al. 2021). However, the analysis did show that the site from the Medanos (Site 5) received less, and much more variable, precipitation than the other sites. This suggests that the intra- and interannual variability of water is an important driver in limiting jaguar density in the Medanos despite ample forest cover and relatively low anthropogenic pressures. As our study areas are at the arid extreme of the jaguar habitat, and our density estimates are consistent with those from protected areas in other dryland systems with high variability in precipitation (Sollmann et al. 2011, 2013; Noss et al. 2012; Gutiérrez-González et al. 2015; Finnegan et al. 2020), our results provide valuable inferences on habitat needs for the conservation of jaguar in arid systems throughout its range and in support of potential reintroduction efforts for jaguars in arid systems such as in the southwestern United States (Sanderson et al. 2021, 2022).

We found no sex effect on either detectability or σ which was consistent with previous modeling that included our data (Thompson et al. 2022), but unexpected compared to general patterns in estimates of jaguar space use from spatial capture–recapture modeling and telemetry data (Sollmann et al. 2011; Tobler et al. 2013, 2018; Boron et al. 2016; Morato et al. 2016; Alvarenga et al. 2021; Thompson et al. 2021). Differences in sex ratios among sites may cause abundance related effects on detectability by sex which collectively offset the effect of sex on detection since both males and females were detected more frequently dependent upon the site (Table 10.1).

We note that our estimates of σ were larger than previous estimates (Thompson et al. 2022) for sites 1–4 which we attribute to differences in the modeling framework, whereby Thompson et al. (2022) explicitly modeled asymmetrical, non-Euclidean space use and connectivity as a function of forest cover, and here we used SCR–RS to estimate habitat driven differences in space use within activity areas. Regardless, both modeling approaches generated similar density estimates, while showing the importance of forest cover for jaguars from different perspectives while reducing potential bias by accounting for asymmetrical space use (Royle et al. 2013a, b; Sutherland et al. 2015).

Although we show a strong selection for forest cover by jaguars, anthropogenic factors negatively affect jaguar survival and occurrence in the Dry Chaco, driving complex source–sink dynamics (McBride and Thompson 2018; Romero-Muñoz et al. 2019, 2020; Thompson et al. 2020). The large movements of jaguars and the maintenance of connectivity in relation to forest loss (McBride and Thompson 2018; Thompson et al. 2021), suggest that the sites with high levels of forest loss are population sinks, with their populations being maintained by immigration (Romero-Muñoz et al. 2019; Thompson et al. 2022). This highlights the importance of considering anthropogenic effects on jaguar occurrence in the Dry Chaco which is further evident in the functional extinction of the jaguar in the Argentine Dry Chaco despite high forest cover and sufficient prey availability (Quiroga et al. 2014; Thompson et al. 2020).

Consequently, our results may not be fully representative of the population trajectory in our study sites. Our sites could be demonstrating extinction debt, whereby individual longevity and immigration are masking negative population trends (Tilman and Lehman 1994; Semper-Pascual et al. 2018; Romero-Muñoz et al. 2019; Thompson et al. 2022). For example, despite similar estimates of density, as well as similarities in anthropogenic influences, the status of the jaguar populations in the more deforested sites (Sites 3 and 4) and in the Medanos (Site 5) is not clear based solely on density estimates. This illustrates the limitations of static estimates of density for conservation evaluations, highlighting the need for long-term studies to quantify survival, recruitment, and immigration to characterize the conservation value of the various landscapes for jaguars (Harihar et al. 2020).

The high rate of forest loss in the Paraguayan Dry Chaco is not only a concern for the conservation of the jaguar, but raises concerns for other forest dependent and endemic species in the Dry Chaco (Romero-Muñoz et al. 2020) such as the Chacoan peccary (*Catagonus wagneri*), Quebracho crested tinamou (*Eudromia formosa*), and Chacoan naked-tailed armadillo (*Cabassous chacoensis*). Furthermore, the forest loss in the Paraguayan Dry Chaco, apart from generating important concerns for biological conservation, has additional cultural and human rights implications as the Paraguayan Dry Chaco is the ancestral lands of multiple indigenous peoples, including the Ayoreo Totobiegosode, the last indigenous peoples outside of the Amazon Basin with members living in isolation (DGEEC 2004).

Considering the jaguar's effective role as an umbrella and flagship for biodiversity conservation (Thornton et al. 2016), its conservation, which is dependent upon forest conservation and the fostering of coexistence, has significant ecological and cultural implications (United Nations Development Program et al. 2019). However, within Paraguay, the jaguar is listed as critically endangered due to continuing high rates of habitat loss and direct human-caused mortality (Giordano et al. 2017), pointing to the urgent need for the Paraguayan government to better implement the national jaguar conservation plan (Secretaría del Ambiente et al. 2016) and national jaguar conservation law (Congreso de la Nación Paraguaya 2014) to ensure the long-term survival of the species and the services that it provides.

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Chapter 11
Abundance of Coimbra-Filho's Titi Monkey in the Atlantic Forest, Brazil: Use of N-Mixture Models for Acoustic Playback Survey Data

Igor Pfeifer Coelho, André Chein Alonso, and Wylde Vieira

Abstract Monitoring the size of local wildlife populations is essential for various purposes, such as controlling pests or invasive species and evaluating conservation strategies. However, accurately estimating the abundance or density of animals can be difficult, especially for unmarked and hard-to-detect species. To overcome these challenges, researchers are increasingly using playback acoustic observations and hierarchical N-mixture models together. In this chapter, we used this approach to estimate the population size of the endangered Coimbra-Filho's titi monkey (*Callicebus coimbrai*), a species endemic to the Atlantic Forest in Brazil. In September 2020, we surveyed 32 sampling sites during 166 sampling occasions using playback calls. We used binomial N-mixture models to estimate the abundance and detection probability of *C. coimbrai* groups in the Mata do Surucucu and Mata do Sabão study areas. Our results showed that the group abundance of *C. coimbrai* increased with forest amount, and group detection decreased with survey time. We estimated 128 groups in Mata do Surucucu and 123 groups in Mata do Sabão. Mean group detection per sampling occasion was 0.33, ranging from 0.44 at 05:57 h to 0.21 at 17:03 h. Considering the mean number of adults per group as three, we estimated a population size of 384 adult individuals in Mata do Surucucu (12.8 individuals/km^2 of forest) and 369 in Mata do Sabão (12.4 individuals/km^2 of forest), indicating a high density of *C. coimbrai* in a region recognized as important for the species' conservation. Our study highlights the usefulness of acoustic playback surveys coupled with N-mixture models in estimating the abundance of elusive and playback-responsive species. We also present considerations on the sampling

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design and the observation method, which can be useful for abundance studies on other species. Overall, this approach can contribute to reliable species monitoring and conservation efforts.

Keywords Acoustic playback · Brazil · Monitoring abundance · N-mixture models

11.1 Introduction

Monitoring the size of local wildlife populations is crucial for many purposes, from the control of pest or invasive species and game management to evaluating species' extinction risk and the effectiveness of conservation strategies. However, accurately estimating the abundance or density of animals can be a hard and expensive task, especially for species that are difficult to detect and unmarked (not marked for individual identification), not suited for the well-established survey and analytical methods such as visual counting of individuals and the distance sampling or capture–recapture analyses (Dénes et al. 2015; McClintock and Thomas 2020). To overcome the low detection of species and lack of individual identification, two important advances in the survey and analytical methods are becoming more used together: playback acoustic observations to acquire count data and hierarchical N-mixture models to account for detectability in abundance estimates.

Many animals vocally respond and/or are attracted to acoustic stimuli, mainly the sounds of their conspecifics or other species (Ladich and Winkler 2017). Acoustic playback is the broadcasting of sounds to provoke a response in animals and is commonly used to study responsive species like birds (De Rosa et al. 2022), marine mammals (Tyack 2009), primates (Fischer et al. 2013), bats (Jones and Siemers 2011), rodents (Wöhr 2018), amphibians (Narins 2018), and insects (Mankin 2012). Playbacks can be used as a survey method to increase the detection in counting the individuals of responsive species, by hearing vocal responses, seeing or capturing attracted individuals. Using playbacks significantly increased the detection of bats (Aylen et al. 2022), squirrels (Downey et al. 2006), dugongs (Ichikawa et al. 2009), amphibians (Schwarzkopf and Alford 2007), and birds (Turcotte and Desrochers 2002; Zuberogoitia et al. 2020a).

In the last two decades, count data from acoustic playback surveys coupled with N-mixture models have become widely used to estimate the abundance of birds (e.g., Dilley 2021; Khamcha et al. 2022; Verdon and Clarke 2022) and sparingly used for other responsive species like lions (Belant et al. 2016) and monkeys (Coelho et al. 2020). N-mixture models (Royle 2004; Royle and Dorazio 2006) belong to a suite of hierarchical models developed to correct for imperfect detection by separating the state process (e.g., occurrence or abundance) and the observation process (detection) in conditionally related models (Kéry and Royle 2016, 2021). By estimating absolute abundance instead of just relative abundance indexes of unmarked species, N-mixture models quickly became widely applied to data from count surveys (Dénes et al. 2015). They are also highly useful in ecology by allowing the simultaneous inclusion of explanatory variables for both abundance and detection processes. Recent studies on the violation of model assumptions and model identifiability (Barker et al. 2017; Link et al. 2018) were followed by important recommendations on the use of N-mixture models (Kéry 2018; Knape 2018; Bötsch et al. 2020).

In this chapter, we present a case study using acoustic playback surveys and N-mixture models to assess the population size of the endangered Coimbra-Filho's titi monkey. We estimated the number of titi groups using repeated counts of groups responding to the playbacks and we then used the mean number of individuals per group to estimate the population size. We hypothesized that the abundance of groups in sampling sites varies according to habitat amount, measured as the percentage of Atlantic Forest cover. We also tested the hypothesis that the detection of titi groups from responses to playback calls varies according to daily time. We present valuable density estimates for this endangered species and discuss considerations on the sampling design and observation method that can be useful for abundance studies on other playback-responsive species.

11.2 Methods

11.2.1 Study Species

Titi monkeys (subfamily Callicebinae; Byrne et al. 2016) are small- to medium-sized (1–2 kg) primates inhabiting South American forests in various regions such as the northern Andes bases, the Amazon, the Atlantic Forest, Caatinga, and Cerrado biomes in Brazil, and the Chacoan forests in Bolivia and Paraguay. Titis live in territorial and small groups, often including only a pair of adults and 1–3 offspring, traveling short daily paths (mean 600–700 m) in their small home ranges (from 0.01 to 0.48 km^2; Bicca-Marques and Heymann 2013). Cryptic and shy, titis are hard to visually detect, but their loud calls for intergroup communication are well known (Caselli et al. 2014) and are the origin of the common names of many Callicebinae species. Titis respond vocally to broadcasted calls and the density of titi species has been recently estimated from playback survey data (Dacier et al. 2011; Gestich et al. 2017; Coelho et al. 2020).

The Coimbra-Filho's titi monkey (*Callicebus coimbrai* Kobayashi and Langguth 1999; Fig. 11.1) is endemic to the Atlantic Forest in Brazil, distributed in a region of about 30.000 km^2 in Bahia and Sergipe states. However, *C. coimbrai* is estimated to occur in just 1% of this region, in small forest patches from 0.03 to about 30 km^2 (Jerusalinsky 2013) and is facing local extinctions of 10% of their populations in recent years (Hilário 2017). Habitat loss is the main threat to Coimbra-Filho's titi, listed as Endangered in the Brazilian and IUCN red lists (Jerusalinsky and Souza-Alves 2018; Jerusalinsky et al. 2020).

Fig. 11.1 Coimbra-Filho's titi monkey (*Callicebus coimbrai*) in Mata do Surucucu and Mata do Sabão study areas in the Atlantic Forest, Brazil. Titi monkeys are playback responsive, and their loud calls can be heard from more than 1 km away in open areas (right)

11.2.2 Study Area

The Atlantic Forest is home to a high number of endemic species and is heavily threatened by habitat loss, named one of the global biodiversity hotspots (Myers et al. 2000). "With broadax and firebrand," the Atlantic Forest has been historically devastated through the economic cycles of timber, sugar cane and coffee plantations, mining, and industrialization (Dean, 1995). Nowadays, only 26% of the original forest cover remains (Rezende et al. 2018), mostly in small patches (< 0.5 km^2) of secondary forest (Ribeiro et al. 2009).

Our study took place in Mata do Surucucu and Mata do Sabão areas in the Atlantic Forest biome, distant 9 km apart from each other in the Sergipe and Bahia states of Brazil (Fig. 11.2). The region includes priority areas for the conservation of *C. coimbrai* (ICMBio 2021; Gouveia et al. 2017). Both areas comprise a main forest patch and surrounding smaller patches embedded in a matrix of pasture and agriculture (Fig. 11.3). They are covered by similar amounts of forest, with 33.9% (30 km^2) of the Mata do Surucucu and 33.4% (29.6 km^2) of the Mata do Sabão covered by forests. We bounded the study areas to include 1.1-km-side hexagons filling a 5 km buffer around the main forest patches, so each study area covers 88.4 km^2 (Fig. 11.2). We choose the hexagon size (3.14 km^2) to represent a similar area to the observed sampling sites.

11.2.3 Playback Surveys

From September 8 to September 29, 2020, we surveyed 32 sampling sites using playback calls. Each site was surveyed on three to seven sampling occasions (visits). We defined a sampling site as a 1 km buffer area around playback points because we can hear titi monkey's responses up to more than 1 km, depending on land cover

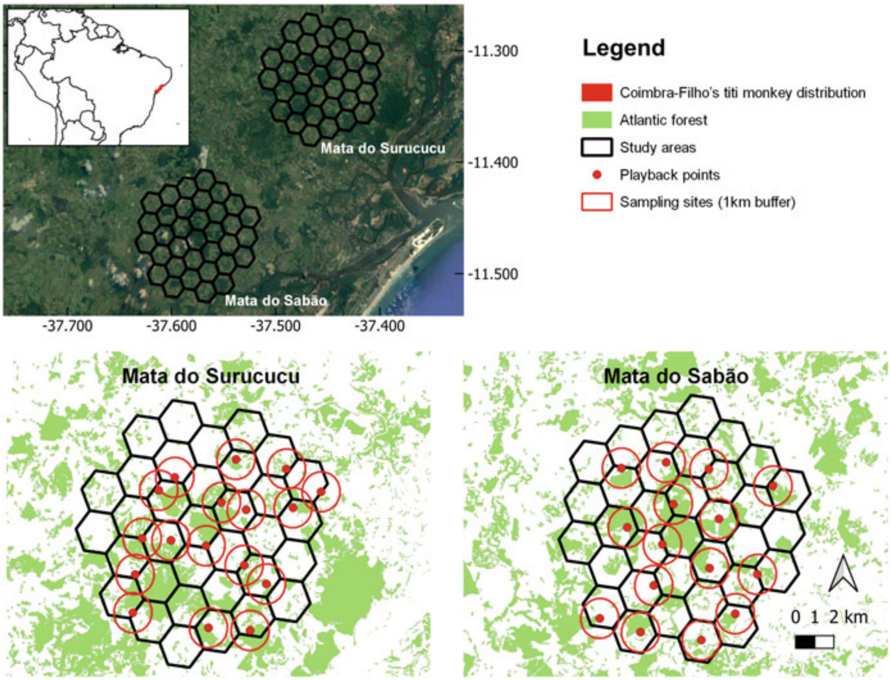

Fig. 11.2 Location of Mata do Surucucu and Mata do Sabão study areas surveyed by playback point counts to estimate the abundance of Coimbra-Filho's titi monkey in 2020

obstruction and topography, though most responses are within 500 m (Coelho et al. 2020; Alonso et al. 2022). In a field test, we could hear the playback call and the response calling of a titi group only up to 500 m in a plain forest cover (Coelho and Alonso, personal observation). Each sampling site covers 3.14 km^2 and could hold five nonoverlapping groups of *C. coimbrai* considered the largest home range known for titi monkeys (0.48 km^2; Bicca-Marques and Heymann 2013). We selected playback sites based on accessibility by roads and trails in the study areas and to keep them 1 km far as possible (Fig. 11.2). Since many sites partially overlapped, we cautiously avoided counting a titi group twice on the same day by registering the direction and loud of responding calls. We acknowledge that our opportunity sampling design is not good practice and probability sampling designs should be used to ensure independent and representative sampling units (Thompson 2012; Smith et al. 2017).

Each sampling occasion consisted of three 1.5 min playback sessions interleaved by 4 min listening periods, totaling 16.5 min of observation per sampling occasion. We used a megaphone (CSR Professional Megaphone SK66 25 W) to play a duet loud call recording performed by free-ranging *C. barbarabrownae*, with approximately 100 dB measured at one meter from the megaphone (Coelho et al. 2020). Two observers, approximately 50 m apart, counted the number of different *C. coimbrai* groups responding during each sampling occasion. We surveyed a given site only once a day, and survey time varied between 05:57 h and 17:03 h. During the study period, sunrise was at 05:28 h and sunset was at 17:27 h.

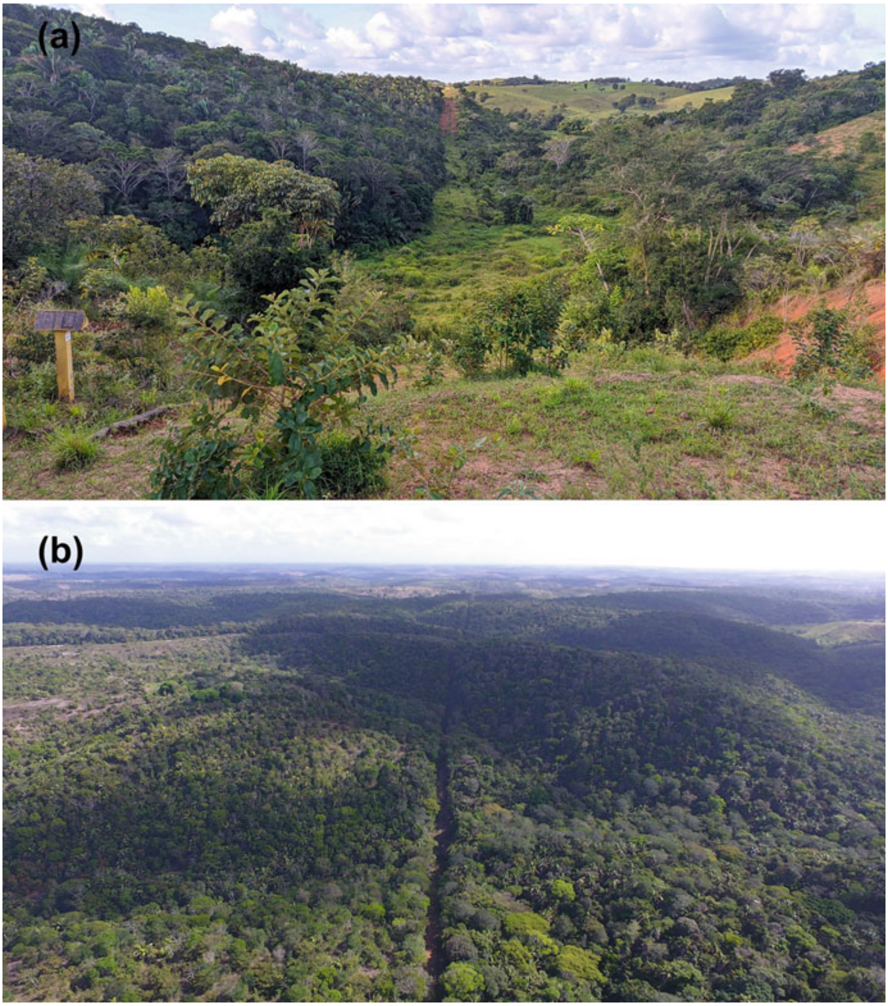

Fig. 11.3 Land cover in Mata do Surucucu (**a**) and Mata do Sabão (**b**) study areas: patches of Atlantic Forest in a matrix of pasture and agriculture

11.2.4 Data Analysis

In N-mixture models, the data consists of repeated counts (multiple sampling occasions, temporal replications) of individuals (in our case, groups of *C. coimbrai*) at multiple sites (spatial replications). Data is modeled as arising from both an abundance process and a detection process. Abundance describes the spatial variation in the number of individuals (or groups, as in our case) among sites using a Poisson (or similar distribution), and detection describes how many of the individuals present at each site are found at each sampling occasion. In the binomial

N-mixture models, there is an assumption that the population being sampled is closed with respect to mortality, recruitment, and movement so that the counts may be viewed as binomial random variables (Royle 2004). N-mixture models account for different numbers of sampling occasions among sites, with the number of occasions affecting the precision of detection and abundance estimates at each site.

We used binomial N-mixture models (Royle 2004; Kéry and Royle 2016) to estimate the abundance and detection probability of *C. coimbrai* groups in the study areas and to test the effects of forest amount on abundance and survey time on detection. We measured forest amount in each of the 32 sampling sites and in each of the 68 hexagons comprising the study areas using QGIS software (QGIS Development Team, 2018) and the *landscapemetrics* package (Hesselbarth et al. 2019) in the R v4.2.1 software environment (R Core Team 2022). We used the land use and land cover maps (30 × 30-m pixel resolution) produced by MapBiomas to calculate the amount of forest (Souza et al. 2020). As titi monkeys call more often in the morning (Price and Piedade 2001; Corsini and Moura, 2014) and detection can be higher at this time (Coelho et al. 2020), we tested the survey time in decimal 24 h format as a quantitative predictor of detection.

We used the *pcount* function from the R package *unmarked* v0.13-0 (Fiske and Chandler 2011) to estimate models' parameters by maximum likelihood. We adopted an information theoretic approach (Burnham and Anderson 2002; Symonds and Moussalli 2011) using Akaike's information criterion corrected for small sample sizes (AICc) to rank competing models using the R package *AICcmodavg* v2.1-1 (Mazerolle 2017). We first tested three different statistical distributions (Poisson, Negative Binomial, and Zero Inflated Poisson) to describe the abundance of *C. coimbrai* groups by competing global models (including all predictors). Poisson model had the lowest AICc, so we adopted this abundance distribution onward. We then competed four models predicting the abundance of *C. coimbrai* groups: a null model (intercept only), a model with abundance as a function of forest amount, a model with detection as a function of survey time, and a global model (including the two predictors).

We ranked models by AICc and by Mean Absolute Error (MAE), as a measure of model predictive accuracy. MAE was measured by leave-one-out cross-validation using the *crossVal* function in the *unmarked* package. We evaluated the sensitivity to the summation limit (K) of the best model by comparing parameter estimates for increasing K (Kéry 2018). The best model fit for our data was assessed by overdispersion metrics, randomized quantile residuals, and graphical diagnostics using the R package *nmixgof* (Knape et al. 2018). Finally, we predicted the number of *C. coimbrai* groups in each hexagon covering the entire study area ($n = 68$) using the *predict* function in the *unmarked* package. We adopted a conservative criterion to define the number of *C. coimbrai* groups in each hexagon by considering 0–0.8 estimated as 0 groups, 0.81–1.8 as 1 group, 1.81–2.8 as 2 groups, and so on. The same criterion was used to define lower and upper confidence limits for the estimates. We estimated the total number of adult *C. coimbrai* individuals in the study area by multiplying the number of estimated groups by 3, the mean number of adults in titi monkey groups. Data and the R script for analysis are available online as supplementary material in the Open Science Framework repository at https://osf.io/9gxqz/.

11.3 Results

We obtained 245 records of *C. coimbrai* groups from 166 sampling occasions in the 32 sites. In only three sites we had no group records, and the maximum number of groups recorded per site in a single occasion varied from one to six. The model including survey time as a predictor of detection and forest amount as a predictor of group abundance was by far the best model ranked by AICc and had the lowest MAE (Table 11.1). The best model showed no sign of a lack of fit to the data or sensitivity to the summation limit.

As expected, the group abundance of *C. coimbrai* increased with forest amount ($\beta = 0.29$; SE = 0.09; 95% CI = 0.11–0.47), and group detection decreased with survey time ($\beta = -2.36$; SE = 0.69; 95% CI = −3.72 to −0.99). The mean number of *C. coimbrai* groups estimated by the best model across the 32 sites was 4.4, ranging from 2.7 groups (95% CI = 1.6–4.3) in the lowest forest amount site to 8.3 (95% CI = 4.9–14.1) in the highest (Fig. 11.4a). Mean detection across 166 sampling occasions was $p = 0.33$, ranging from $p = 0.21$ (95% CI = 0.13–0.31) at 17:03 h to $p = 0.44$ (95% CI = 0.29–0.61) at 05:57 h, the earliest survey time (Fig. 11.4b).

Using the best model to predict the abundance of *C. coimbrai* groups across the 68 hexagons covering the study areas and applying the conservative rounding criterion produced an estimate of 128 groups (95% CI = 81–192) in Mata do Surucucu and 123 groups (95% CI = 79–195) in Mata do Sabão (Fig. 11.5), resulting in group densities of 4.2 (95% CI = 2.7–6.4) and 4.1 (95% CI = 2.6–6.5) groups/km^2 of forest habitat, respectively. Considering the average

Table 11.1 Competing N-mixture models predicting Coimbra-Filho's titi monkey group abundance in Mata do Surucucu and Mata do Sabão areas in the Atlantic Forest, Brazil

Model	Meaning	*K*	LogLik	ΔAIC_c	Weight	MAE
$\lambda \sim$ FA, $p \sim$ T	Abundance varies according to forest amount in the site, detection varies according to survey time	4	−236.09	0	0.96	1.08
$\lambda \sim 1$, $p \sim$ T	Abundance does not vary among sites, detection varies according to survey time	3	−240.67	6.55	0.04	1.11
$\lambda \sim$ FA, $p \sim 1$	Abundance varies among sites according to forest amount in the site, detection does not vary among sites and sampling occasions	3	−242.44	10.08	0.01	1.11
$\lambda \sim 1$, $p \sim 1$	Abundance does not vary among sites, detection does not vary among sites and sampling occasions	2	−247.44	17.65	0	1.17

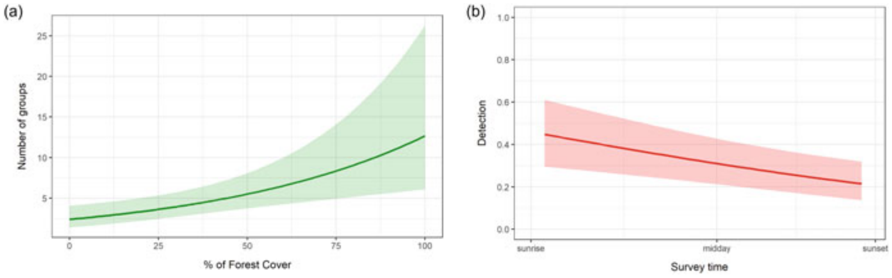

Fig. 11.4 Predicted relations of the number of groups of *Callicebus coimbrai* and forest cover (**a**), and of the detection of groups from playback responses and survey time (**b**)

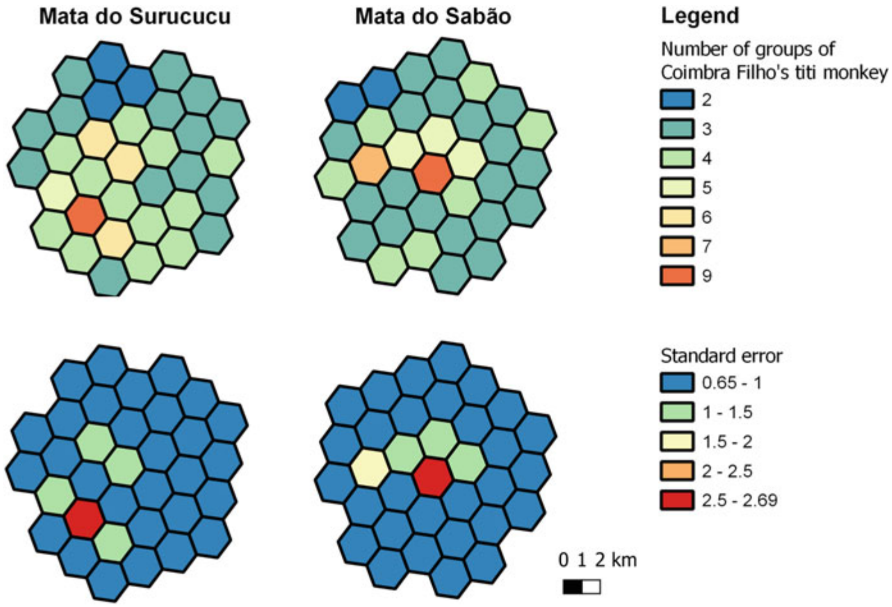

Fig. 11.5 Number of groups of *Callicebus coimbrai* estimated in Mata do Surucucu and Mata do Sabão study areas using a N-mixture model. The abundance of groups varies as a linear function of forest cover and detection varies linearly with survey time

group size of 3 adults, we estimated a local population size of 384 adult individuals (95% CI = 243–576) in Mata do Surucucu, resulting in a density of 12.8 individuals/km^2 of forest (95% CI = 8.1–19.2). In Mata do Sabão, we estimated a population of 369 individuals (95% CI = 237–585) and a density of 12.4 individuals/km^2 of forest (95% CI = 8–19.7).

11.4 Discussion

We used data from acoustic playback surveys and N-mixture models to estimate the abundance of the endangered Coimbra-Filho’s titi monkey in Mata do Surucucu and Mata do Sabão areas in the Atlantic Forest, Brazil. Our results of 4 groups/km^2 and 12 individuals/km^2 in each area indicate a high density of *C. coimbrai* in a region recognized as important for the species’ conservation (ICMBio 2021; Gouveia et al. 2017). Considering estimates from visual counts in line transects analyzed by distance sampling models, the density of titi species in the Atlantic Forest rarely exceeds 10 individuals/km^2 (see Table 4 in Chagas and Ferrari 2011 and references therein). The only published estimate of *C. coimbrai* density analyzed by distance sampling (accounting for detectability) indicates 9.2 groups/km^2 and 22.1 individuals/km^2 (using a mean group size of 2.4 individuals) in Fazenda Trapsa, an area covered by 3.5 km^2 of forest patches about 40 km distant from Mata do Surucucu (Chagas and Ferrari 2011). These density estimates of *C. coimbrai* indicate unexpectedly high abundance, as for other titi species evaluated considering detectability (Dacier et al. 2011; Coelho et al. 2020). Shy and cryptic, titi species can be elusive to visual counts, rarely yielding enough data to apply distance sampling estimates and giving the impression of being rare when in fact visual detection is low. Acoustic playback survey data collected to be analyzed with N-mixture models (hereafter PbsNmix) can be a reliable approach to precisely estimate the abundance of elusive and playback-responsive species. We now present considerations on the sampling design and the observation method to the PbsNmix approach.

11.4.1 Defining the Study Area, Sampling Sites, and Sampling Occasions

As for any scientific study, a probability-based sampling design should be adopted for selecting the location of sampling sites in the study area (sampling universe or population), the area for which we want to estimate abundance (Anderson 2001; Thompson 2012; Smith et al. 2017). Opportunity sampling is still commonly adopted in ecology because of the difficulties involved with accessing areas and learning to use appropriate software for sampling design (Smith et al. 2017). However, it is possible to redefine the study area excluding difficult-to-access areas after a preliminary field inspection, and software for sampling design are increasingly available (Foster 2021; Dumelle et al. 2022). Though we used opportunistic sampling in this chapter and in a previous PbsNmix study (Coelho et al. 2020), it is feasible to adopt a probability sampling even in hard-to-reach areas, as we are experiencing in an ongoing study adopting PbsNmix approach (https://www.speciesconservation.org/case-studies-projects/blond-titi-monkey/27289).

Besides accessibility, the study area should be large enough considering the size and minimum number of sampling sites to allow inference. A sampling site should be large enough to contain the home range of some individuals (or groups) and can be totally or partially observed, but we rarely know the effective observed area (Kéry and Royle 2016). In acoustic playback surveys, the effective observed area depends on sound propagation and, in some cases, on the species' capacity to reach the observer (when playbacks are used to attract individuals to visual count or capture, see Belant et al. 2016). Estimating the effective observed area by playback points can be done by field experiments or possibly modeling sound propagation using land cover and topography. For example, Ogutu and Dublin (1998) observed the response of lion groups to broadcasts from various distances, indicating a range of 2.5 km within which lions would respond. It is reasonable to represent a site by a single playback point when individuals (or groups) can be counted from large areas, as in our case that titi monkeys respond to calls up to more than 1 km. However, in some cases, the effective observed area by a playback point is presumably small relative to the species' home range, such as the area of no more than 200 m-radius estimated for marmosets (Carmo 2022). A possible alternative design for such cases is to define large sites (squares or hexagons) to be surveyed by many playback points selected randomly in each site. To avoid double counting individuals in the same site and sampling occasion, playback points in the same site could be done simultaneously or in short intervals by using two or more field crews.

When defining the study area, one should consider that it is recommended at least 20 sampling sites for inference from N-mixture models (Kéry and Royle 2016). During the design of a sampling scheme, simulations should be used to indicate the number of sampling sites and sampling occasions considering possible values of abundance and detection (see chapter 6.6 in Kéry and Royle 2016 for R code). Only after considering minimum sample sizes to achieve unbiased estimations of abundance, one should add cost and feasibility in the study planning, otherwise any resource and time invested can be lost by ending up with noninformative data.

11.4.2 Improving Detection in Acoustic Playback Surveys

Abundance hardly can be estimated by any analytical method when the detection of individuals is very low (Couturier et al. 2013), thus maximizing detection of the observation method is imperative in many situations. Detection of acoustic playback surveys can be improved by using the most attractive acoustic stimuli (type, broadcast devices, volume), increasing the time of broadcastings and the time of observation per sampling occasion, sampling at the species' preferred time of response, and using trained observers. Studies comparing variables affecting detection are very important to guide playback surveys. For example, ungulate species responses are stronger following playback of baboon alarm calls than contest calls

(Kitchen et al. 2010). Although a study found that the type of call (feeding x social call) and type of device had no effect on capture rates of bats (Aylen et al. 2022), broadcast devices should be chosen, when possible, according to known hearing and vocal frequency bandwidth limits of target species (De Rosa et al. 2022).

The total time of broadcasting per sampling occasion can increase detection, as a fourfold increase in the detection of owls was observed when comparing five to fifteen-minute playbacks (Zuberogoitia et al. 2020b). Increasing the time of observation (duration of each sampling occasion, including broadcastings) from 3 to 10 min resulted in 55% greater detection of the Northern bobwhite (Lituma et al. 2017). The time of observation should be longer in cases when individuals are attracted to the playback point for visual counts, as the 70-min survey for lions as they can come from up to 3 km away (Belant et al. 2016). The duration of sampling occasions should be defined considering first a good enough detection value, and second the total study period and cost.

More training of the observers to find and correctly identify species' responses before surveys can be important, as shown by the increased detection of owls and nightjars by experienced observers (Zuberogoitia et al. 2020a). Moreover, restricting surveys to the periods of higher calling or movement activity of the individuals can improve the detection of many species. Studies have shown that detection is related to survey time, as found for titi monkeys that emit long calls especially in the early morning (this study; Coelho et al. 2020), and nocturnal birds with higher detection at the first hours after sunset (Zuberogoitia et al. 2020a). Though controlling variables to improve detection can be imperative for estimating abundance in some cases, one option when they are unknown or increase study cost prohibitively is to include them as covariates in N-mixture models.

11.5 Conclusions

In this chapter, we present estimates on the abundance of the endangered Coimbra-Filho's titi monkey using data from acoustic playback surveys analyzed with N-mixture models. Our results are very important to the species' action plan aiming to promote the viability of *C. coimbrai* populations (ICMBio 2018). Accessing the size of local wildlife populations by considering detectability is crucial for reliable species monitoring. Acoustic playback surveys coupled with N-mixture models are a useful approach for elusive and playback-responsive species.

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Chapter 12
Modeling Density and Habitat Preferences of the Mountain Tapir (*Tapirus pinchaque*) in Northern Peru Using Spatial Mark-Resight and Occupancy Models

José Luis Mena, Jorge Rivero, and Mathias W. Tobler

Abstract The mountain tapir (*Tapirus pinchaque*) is one of the largest Neotropical mammals, with a distribution restricted to montane cloud forest and paramo habitats in the northern Andes. This tapir is classified as Endangered on the IUCN Red List, is also included in CITES Appendix I, and is considered Critically Endangered in Peru. It is threatened by habitat loss and fragmentation as well as hunting throughout its range. Despite its important ecological role, there is little information available about its population ecology. We conducted camera-trapping surveys (60–85 stations), for a total of 23,723 camera-days between 2014 and 2017, during both wet and dry seasons, along elevations from 1600 to 3600 m above sea level at the Tabaconas Namballe National Sanctuary (TNNS) in northern Peru. We estimated a density between 5.87 ind/100 km^2 and 9.55 ind/100 km^2. Habitat preferences of mountain tapirs appear to be explained by both distance to villages and slope.

Keywords habitat preferences · Mountain tapir · occupancy · Peru · spatial mark-resight model · *Tapirus pinchaque.*

12.1 Introduction

Tapirs play important roles in the functioning of ecosystems, as they are both seed predators and important seed dispersers for a wide diversity of plant species across tropical forests (Tobler et al. 2010; Chalukian et al. 2013; Giombini et al. 2016). Particularly, Neotropical tapirs appear to have a unique role as long-distance

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Fig. 12.1 Mountain tapirs (*Tapirus pinchaque*) moving across Tabaconas Namballe National Sanctuary in the northern Peruvian Andes. (Photograph by WWF-Peru)

dispersers of large seeds (O'Farrill et al. 2013). Like other large herbivore species, tapir populations and their geographical range are shrinking due to hunting, land use change, and negative interactions with livestock (Ripple et al. 2015, 2016). The mountain tapir (*Tapirus pinchaque*) is the smallest of the three American tapir species (Padilla et al. 2010) and occurs from 2000 to 4500 m in the Andes of Colombia, Ecuador, and Peru, where its presence is associated with montane cloud forest, paramo, and scrub ecotone (Schauenberg 1969; Lizcano and Cavelier 2000a; Hutchins et al. 2003; Fig. 12.1). It is the most threatened large mammal of the northern Andes (Cavelier et al. 2010; More et al. 2022) and is classified as Endangered in the IUCN red list and included in CITES Appendix I (Lizcano et al. 2016). The main threats to the mountain tapir are hunting, illegal trade for body parts, and accelerated habitat destruction and fragmentation, which have led to population declines in most of its historic range (Cavelier et al. 2010; Padilla et al. 2010). Optimistic estimates of mountain tapir population sizes suggest between 5000 and 5700 individuals remaining in the wild (Cavelier et al. 2010), but the numbers are likely much lower – perhaps as few as 2500 individuals throughout their range (Lizcano et al. 2016). Unfortunately, data on the abundance and population ecology of this species is still limited (Ripple et al. 2015), and there is only one published study that estimated density, based on footprints (Lizcano and Cavelier 2000a, 2000b).

Accurate estimates of the distribution, habitat preferences, abundance, and population trends of endangered species such as the mountain tapir are important for assessing extinction risks and for evaluating management actions. A few studies have used line transect sampling to estimate population densities of the lowland tapir (*Tapirus terrestris*) (Trolle et al. 2008; Ferreguetti et al. 2017) and Baird's tapir (*Tapirus bairdii*) (Lira et al. 2004; Naranjo and Bodmer 2007), but in some cases the low detectability of individuals has precluded the use of this technique (Endo et al. 2009). In addition, the elusive behavior and the difficult topography of the Andes add more challenges to the use of line transect sampling for the mountain tapir.

Camera trapping offers an alternative noninvasive tool for estimating population densities (Ahumada et al. 2013; Rovero et al. 2014; Rich et al. 2017). This technique, paired with mark-recapture analyses, provides estimates of densities when animals can be individually recognized by marks (O'Connell et al. 2011). Spatial capture–recapture (SCR) models are widely used for species where individuals can be distinguished by natural marking such as jaguars or tigers (Tobler and Powell 2013; Karanth and Nichols 2017). SCR has also been used to estimate population density of several species of tapirs such as Baird's tapir (Rivero et al. 2021), lowland tapir (Tobler et al. 2014), and Malayan tapir (*Tapirs indicus*) (Rayan et al. 2012) where individuals were identified based on marks and deep scarring on the body, wrinkles on the neck and belly, damage to the ears, ear shape and notches, skin marks, tail length and shape, sex, size, and shape and size of testicles, among others. However, the identification of individual tapirs based on visible natural markings is a difficult task to accomplish and depending on the environment and image quality is not always possible. There are several other abundance estimation methods that have been proposed for different sampling conditions (Iijima 2020; Gilbert et al. 2021). For cases where only a portion of individuals can be identified (i.e., only some individuals have been marked), it is possible to apply spatial mark-resight models (Chandler and Royle 2013; Efford and Hunter 2018). When it is not possible to identify individuals at all, one can run a spatial model that uses the correlation between presence–absence data to estimate density (Chandler and Royle 2013; Ramsey et al. 2015). In addition, camera traps in combination with occupancy models (MacKenzie et al. 2002), are also widely used to assess the distribution and habitat preferences of large mammals (O'Connell and Bailey 2011), including tapirs (Tobler et al. 2009; Mena et al. 2020; Martinez et al. 2021).

In this study, our aim was to estimate the population density of mountain tapirs in a protected area in Northern Peru. Furthermore, we assessed environmental and anthropogenic factors that influence the distribution of mountain tapirs in the study area using an occupancy model. Specifically, because tapirs tend to avoid areas with high human density (Downer 1996; Padilla et al. 2010), we expected a negative relationship between tapir presence and habitat disturbance. In addition, as mountain tapirs are confined to high elevations from 2000 to 4500 m (Lizcano and Cavelier 2000a), we expected a positive relationship between tapir presence and elevation. Overall, our study provides the first estimation of mountain tapir density in Peru as well as key information on the current status of this population and its habitat use in northern Peru.

12.2 Methods

12.2.1 Study Site

This study took place in the Tabaconas Namballe National Sanctuary (TNNS) and its buffer zone (79°24′–79°06′W, 5°00′–5°20′S) in the northern Andes of Peru (Fig. 12.2). The TNNS is a protected area of 32,124 hectares with an elevation gradient between 1600 and 3600 m. Average annual temperatures range from 11.2 to 24.6 °C, and annual rainfall fluctuates between 1490 and 1770 mm, with the rainy season usually occurring from November to March. The TNNS is characterized by two main vegetation types: paramo (>3000 m) with tall and dense tussock grasses and shrubs (Fig. 12.3), and montane forest (1600–3000 m) with canopy height of 10–25 m, dominated by tree species belonging Neotropical Podocarpaceae (e.g., *Podocarpus* and *Prumnopitys*), among others. More details about the study area are given in Mena and Pacheco (2020).

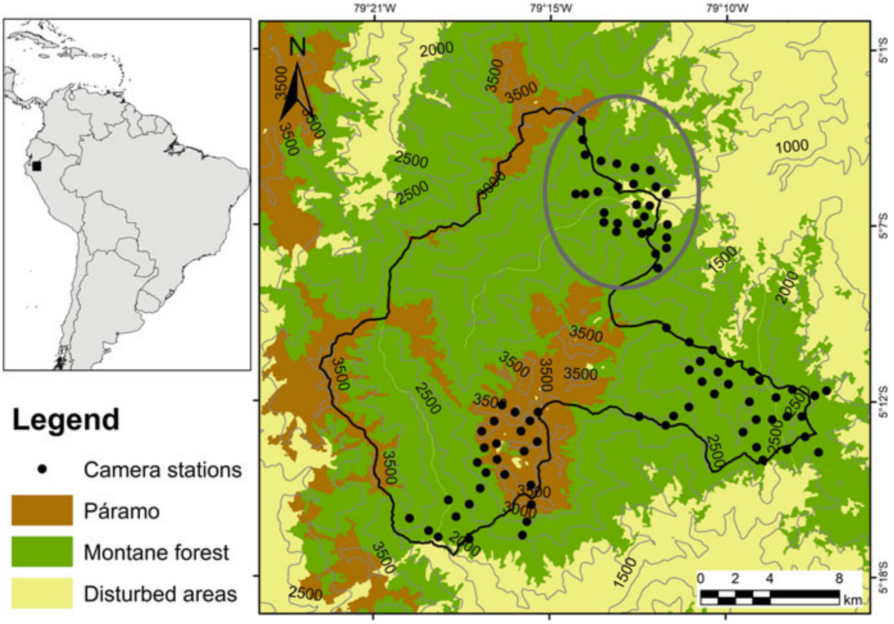

Fig. 12.2 Study area in the Tabaconas Namballe National Sanctuary (TNNS), Peru. The gray circle highlights additional sites included in the 2016 survey (see Table 12.1)

Fig. 12.3 View of the high-altitude paramo, habitat of the mountain tapir in Tabaconas Namballe National Sanctuary, Peruvian Andes. (Photograph by Jose L. Mena)

Table 12.1 Information about the four surveys carried out in the Tabaconas Namballe National Sanctuary, Peru

Session	Season	Start	End	Days	Sites	Camera-days	Det	Polygon size (km^2)
2014–2015	Wet	16 Nov 2014	24 April 2015	160	67 (0)	6993	105	156
2015	Dry-Wet	28 Aug 2015	19 Nov 2015	84	61 (14)	3793	83	164
2016	Dry	24 June 2016	15 Sept 2016	120	85 (48)	8516	87	317
2017	Dry-Wet	12 Sept 2017	04 Dec 2017	102	60 (58)	4721	62	162

Photos indicate the number of photos of tapirs taken. Detections (Det.). In parenthesis, the number of sites with two camera traps

12.2.2 Camera Trapping

We conducted camera-trap surveys during the dry season of 2015, 2016, and 2017, and the wet season of 2014–2015 (Fig. 12.2). Each survey consisted of a grid of 51–85 sites with a spacing of ~1 km based on a systematic design stratified by vegetation type and elevation (Mena and Pacheco 2020). One camera trap (Bushnell® Trophy Cam) was set at each site approximately 40 cm above the ground. Cameras were unbaited and active 24 h per day. All images were managed in Camera Base 1.7 (Tobler 2015). Detailed information on each survey is given in Table 12.1.

12.2.3 Density Estimation

To estimate tapir densities for the four surveys, we used a spatial mark-resight (SMR) model for detection/nondetection data (Chandler and Royle 2013; Ramsey et al. 2015). SMR models combine information from marked individuals with detection data from unmarked individuals. The marked portion of a SMR model is analog to a spatial capture–recapture model (Borchers and Efford 2008; Royle and Young 2008; Efford et al. 2009) with the data y_{ik}, being the number of detections of individual $i = 1, 2\ldots$m at camera station $j = 1, 2\ldots J$. This was modeled as:

$$y_{ij} \sim \text{Binomial}\left(K_j, p_{ij}\right)$$

where K_j is the number of days in which station j was active and p_{ij} is the detection probability for individual i at station j. The detection probability p_{ij} at the coordinates x_j was modeled as a half-normal detection function with parameters $g0$, the detection probability at the activity center s_i, and σ, the scale parameter, as:

$$p_{ij} = g_0 \ \exp\left(-\frac{1}{2\sigma^2} \left\|x_j - s_i\right\|^2\right)$$

We created encounter histories for recognizable (marked) individuals. Markings used for individual recognition included obvious deep scarring on the body, ear notches, wrinkles on the belly, skin marks, sex, and size. All individuals were identified by JLM and JR. We extracted metadata from camera-trap images and constructed encounter histories for the marked individuals from Camera Base (Tobler 2015). Since we had to observe an individual at least once in order for it to be "marked," all-zero capture histories for marked individuals were not possible. This could lead to an overestimation of detection probabilities and therefore an underestimation of densities. We therefore ran a second model for comparison that used data augmentation for the marked part of the model (Royle et al. 2014), analogous to a SCR model.

The data for the unmarked portion of the model were the number of days n_j out of K_j days an unmarked tapir was detected at station j. These were modeled as:

$$n_j \sim \text{Binomial}\left(K_j, P_j\right)$$

where P_j, the probability that at least one unmarked individual $u = 1, 2\ldots M$ was detected at station j, is

$$P_j = 1 - \prod_{u=1}^{M} \left(1 - p_{uj} z_u\right)$$

We used data augmentation to estimate the number of unmarked individuals u with the variable z_u indicating whether an individual was in the population or not.

$$z_u \sim \text{Bernoulli}(\Psi)$$

where Ψ is the proportion of the M augmented individuals that is available for detection. The detection parameters $g0$ and σ are shared between the marked and unmarked models and marked individuals provide most of the information needed to estimate these parameters. The estimated population size $\widehat{N}$ is then the sum of all unmarked individuals plus the observed, for the model without data augmentation, or estimated, for the model with data augmentation, number of marked individuals (Royle et al. 2014):

$$\widehat{N} = \sum_{u=1}^{M} z_u + \widehat{m}$$

and the density is estimated as $\widehat{D} = \widehat{N}/A$ where A is the area of the state space, an area larger than the trap array over which the activity centers are modeled.

Unfortunately, we were only able to reliably identify individuals in the 2015 survey, due to a lack of distinct markings on animals for the other years. In order to be able to estimate densities for all surveys and leverage all information collected across the years, we constructed a mutisession model where the data from all surveys $t = 1,2,\ldots,T$ were combined into a single model (Tobler et al. 2014). We did this by stacking the data and estimating a survey-specific inclusion probability Ψ_t. We assumed that detection parameters $g0$ and σ were constant across surveys. As we had a relatively small number of marked individuals, we ran the same models with an informative prior for σ following Chandler and Royle (2013). Based on the limited information on mountain tapir home range size (Downer 1996; Lizcano and Cavelier 2004; Castellanos 2013), we assumed home range size between 2.5 and 10 km^2 and therefore chose a prior of $\sigma \sim$ Gamma (80,150). For all other parameters we used uniform priors. We fitted SMR models in R using JAGS (Plummer 2003). The Bayesian models were run with three chains of 30,000 iterations each and a burn-in of 15,000 iterations. Model convergence was assessed by checking that the Gelman–Rubin diagnostic statistic was <1.1 for each parameter (Gelman et al. 2014).

12.2.4 Occupancy Analysis of Habitat Use

To estimate tapir occupancy and habitat use we analyzed the data with a multisession Royle–Nichols occupancy model (Royle and Nichols 2003). For point sampling of mobile animals such as mountain tapirs we interpret occupancy as the probability of a site being used (i.e., habitat use) and the Royle–Nichols model can better accommodate differences in the intensity of use across sites. Occupancy modeling presents general assumptions, and we considered that those assumptions were met in our study (MacKenzie et al. 2018). Thus, we assumed that occupancy status at each site did not change during the sampling period, and variation in occupancy and detection probability were accurately modeled with covariates.

We used vegetation type (forest or paramo), elevation, slope, distance to villages (as a proxy of disturbance), and distance to water sources as occupancy covariates. We quantified the covariates in a circular buffer (250-m radius) around each sampling site. Variables were standardized to have a zero mean and unit variance to facilitate the interpretation of relative effect sizes (Kéry and Royle 2016). All GIS calculations were done in ArcMap (ESRI*ArcGIS 10.5, Redlands, California-ESRI, 2018). We tested covariates for collinearity (Zuur et al. 2013) using the variance inflation factor (VIF) in the *HH* package (Heiberger and Holland 2015) in R (R Core Team 2022). All covariates were minimally correlated (VIF < 3). We also tested if detection probability varied by session. We used the Akaike Information Criterion corrected for small samples ($\Delta\mathrm{AIC_c} \leq 2$) to select the best models, and w_i (the $\mathrm{AIC_c}$ weight) to assess the relative explanatory power for each model. In addition, to estimate the relative importance of each variable included in any of the top-ranked models, we estimated the sum of Akaike weights of these models (w_{all}) (Burnham and Anderson 2002). Data analysis was conducted in R (R Core Team 2022) with the *unmarked* package (Fiske and Chandler 2011). We used the *AICcmodavg* library (Mazerolle 2019) to assess the adjustment fit (*P*) with 10,000 parametric bootstrap replications.

12.3 Results

We obtained a total of 3681 pictures of mountain tapirs with 337 independent detections (see Table 12.1). We identified 10 adult individuals in the survey of 2015 (three males and seven females), which had a total of 46 recaptures. As expected, the mean estimated density was lower for models without data augmentation for marked animals and for the uninformative prior for σ (Table 12.2). The mean estimated density ranged from 5.87 ind/100 km^2 to 9.55 ind/100 km^2; σ ranged from 801 to 996 m, and $g0$ ranged from 0.036 to 0.041 (Fig. 12.4). For models with data augmentation, the density estimate was higher for the year with marked individuals (2015) than for the other year.

Table 12.2 Mountain tapir density in ind/100 km^2 estimated with Bayesian multisession Spatial Mark-Resight models with different parameterizations, including no data augmentation or data augmentation for marked individuals, and the use of an uninformative uniform prior or an informative gamma prior for the σ parameter

Uninformative σ Prior						
		Mean	SD	LCI	UCI	CV
No Aug.	D 2014–15	5.80	1.93	2.76	10.17	0.33
	D 2015	6.39	1.76	3.54	10.39	0.28
	D 2016	5.06	1.54	2.54	8.62	0.30
	D 2017	6.25	2.01	2.87	10.72	0.32
	D mean	5.87	1.14	3.90	8.38	0.19
	$g0$	0.036	0.005	0.027	0.047	0.14
	σ	996	71	866	1145	0.07
Aug.	D 2014–15	6.40	2.11	2.99	11.17	0.33
	D 2015	11.65	2.63	7.19	17.47	0.23
	D 2016	5.60	1.62	2.87	9.29	0.29
	D 2017	6.80	2.13	3.32	11.61	0.31
	D mean	7.61	1.34	5.25	10.42	0.18
	$g0$	0.036	0.005	0.027	0.046	0.14
	σ	955	66	836	1094	0.07
Informative σ Prior						
		Mean	SD	LCI	UCI	CV
No Aug.	D 2014–15	7.74	2.30	3.98	12.94	0.30
	D 2015	7.65	2.09	4.20	12.38	0.27
	D 2016	6.90	1.84	3.76	11.06	0.27
	D 2017	8.28	2.42	4.20	13.71	0.29
	D mean	7.64	1.28	5.36	10.39	0.17
	$g0$	0.041	0.005	0.032	0.053	0.13
	σ	820	42	743	905	0.05
Aug.	D 2014–15	8.30	2.41	4.20	13.71	0.29
	D 2015	13.88	2.97	8.73	20.23	0.21
	D 2016	7.33	1.95	4.09	11.61	0.27
	D 2017	8.69	2.46	4.53	14.16	0.28
	D mean	9.55	1.43	6.97	12.52	0.15
	$g0$	0.040	0.005	0.031	0.051	0.13
	σ	801	40	726	885	0.05

The top-ranking occupancy model showed that mountain tapir habitat use was significantly and positively correlated with the distance to villages ($\beta = 0.288 \pm 0.08$) (Table 12.3), and negatively with slope ($\beta = -0.408 \pm 0.089$, Fig. 12.5). The model exhibited evidence of adequate fit ($P = 0.32$). There were significant differences in detection probabilities across survey sessions (Fig. 12.5). The estimated mean occupancy was 0.47 ± 0.07 (0.40–0.55) and the mean detection probability was 0.019 ± 0.002 (0.015–0.023).

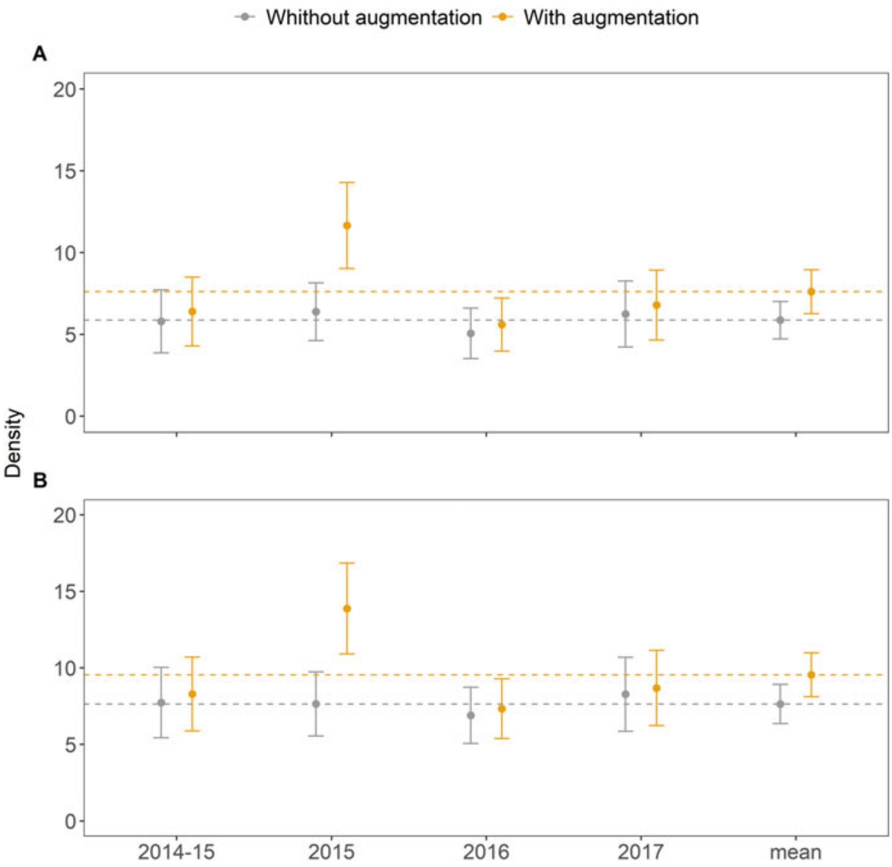

Fig. 12.4 Density estimates for mountain tapirs from four camera-trap surveys in the Tabaconas Namballe National Sanctuary using a multisession spatial mark-resight model. Density in ind/100 km^2. (**a**) Uninformative σ Prior and (**b**) Informative σ Prior

Table 12.3 Top five occupancy models fitted with the Royle–Nichols models for the mountain tapir (*Tapirus pinchaque*)

Model	AIC	ΔAIC	*w*	N par	−2l
λ(dist$_{\text{villages}}$ + slope) *r*(.)	1965.30	0.00	0.90	7	−975.44
λ(elevation + slope) *r*(.)	1971.88	6.58	0.03	7	−978.73
λ(habitat + slope) *r*(.)	1971.93	6.63	0.03	7	−978.75
λ(slope) *r*(.)	1973.06	7.76	0.02	6	−980.37
λ(season + slope) *r*(.)	1974.73	9.43	0.01	7	−980.15

λ: average abundance per site, *r*: per-individual detection probability, AIC: Akaike information criterion, ΔAIC: difference in AIC values between each model and the best model; *w*: AIC model weight; N Par: number of parameters; −2l: twice the negative log-likelihood. Covariates: distance to villages (distance$_{\text{villages}}$), slope (slope) and distance to water sources (distance$_{\text{water}}$)

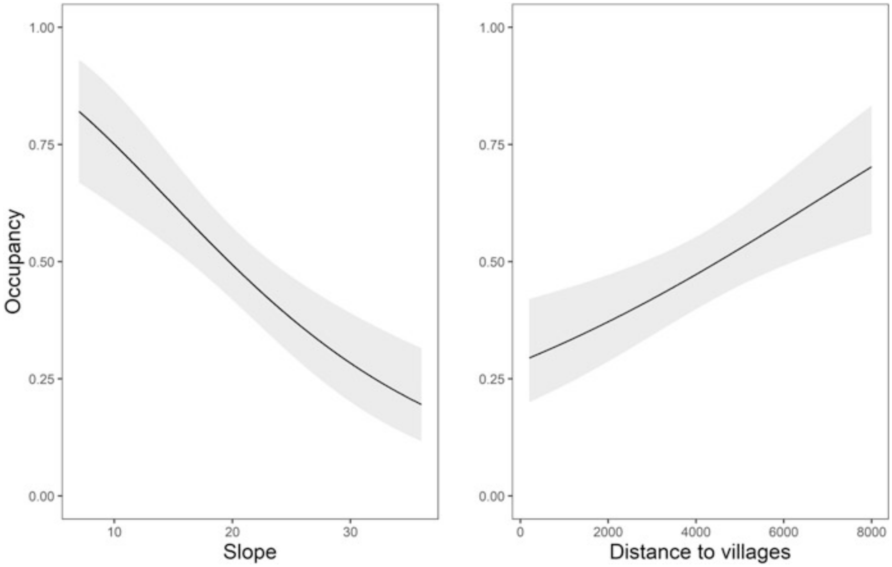

Fig. 12.5 Estimated covariate relationships in the site-occupancy model for mountain tapirs at the Tabaconas National Sanctuary. Gray lines show the 95% CIs

12.4 Discussion

We have provided the first estimates of mountain tapir density based on a spatial mark-resight model. While spatial capture–recapture models are the standard for estimating densities of species with individual markings from camera-trap data and have been successfully applied to tapirs before (Rayan et al. 2012; Tobler et al. 2014), identifying individual mountain tapirs was more challenging than other tapir species due to their longer fur that covers many marks such as scares, skin patches, and skin folds. Spatial mark-resight models allow for the identification of a subset of individuals, for example, based on distinct and easily visible ear notches without the need for discarding information from animals that lack such markings. While in some cases density can be estimated from spatial captures of unmarked individuals alone, simulations by Chandler and Royle (2013) have shown that marking a subset of individuals can substantially increase the precision of the estimate and in some cases might even be required to successfully estimate parameters such as $g0$, σ or N (Chandler and Royle 2013; Sollmann et al. 2013). Combining data from multiple years into a multisession model allows for sharing parameters across years and thus leveraging the combined dataset with a positive impact on precision. Multisession models also allow for an easy estimation of population trends over time, something needed for monitoring programs. Other methods exist for estimating abundance or density from camera-trap data from unmarked individuals. The random encounter model (Rowcliffe et al. 2008; Carbajal-Borges et al. 2014) has been used to estimate tapir density before (Carbajal-Borges et al. 2014; Rivero et al. 2021) but the model requires an estimate of movement speed that is generally not available for a particular study area and density estimates often have a low precision. Furthermore, simulations showed that the model is sensitive to the violation of the assumption of constant movement speed (Santini et al. 2022).

Our mean density estimates of 5.9–9.6 ind/100 km^2 are much lower than an estimate of 32 ind/100 km^2 for lowland tapirs in French Guiana (Tobler et al. 2014), and an estimate of 58 ind/100 km^2 for the same species from the Pantanal of Brazil (Trolle et al. 2008). Both studies were conducted in lowland habitats with a much higher primary productivity than the montane cloud forest and paramo habitats of this study. More comparable density estimates were found for Baird's tapir in northern Colombia with 10.2 ind/100 km^2 (Mejía-Correa et al. 2014), the Lacandon Forest in Mexico with 5–24 ind /100 km^2 (Naranjo and Bodmer 2007), and in the Sierra Madre de Chiapas, Mexico with 10.0 ind/100 km^2 (Rivero et al. 2021), as well as for the Malayan tapir in Peninsular Malaysia with a density of 9.5 ind/100 km^2 (Rayan et al. 2012). A few studies have estimated mountain tapir densities using methods other than camera traps. Downer (1996) estimated a minimum of 17 ind/100 km^2 based on extrapolations from an individual home range using radiotracking collars in Sangay National Park, while Lizcano and Cavelier (2000a) estimated 18 ind/100 km^2 based on a tracking census and a multivariate analysis for individualization in Parque Nacional Natural Los Nevados, Colombia. The coefficients of variation (CV) for our estimates ranged from 0.27 to 0.32, which were slightly higher than what is desirable for monitoring purposes (Morin et al. 2022), but still acceptable given the limitation of the data. Using an informative prior for σ only lead to a slight reduction of the CV.

Density estimates were very stable across years for the models using no data augmentation but were higher for the year with marked individuals when using data augmentation. While from a theoretical point of view data augmentation should be applicable for our data since there were no known marked individuals that were never captured, our marking process also violated the assumption that individuals were marked across the state space (Royle et al. 2014). How this interacts with data augmentation will require further studies.

Based on the movement parameter σ, we can estimate an approximate home range size, assuming a circular home range, of 12.1–18.7 km^2. This is considerably larger than the 95% kernel home range of 2.9 km^2 estimated for a male tapir in Colombia by Lizcano and Cavelier (2004), 3.97 km^2 (range 0.62–9.16 km^2) in Cayambe Coca National Park by Castellanos (2013), and the "core area" of 7.7–10.2 km^2 estimated for three individuals in the Sangay National Park, Ecuador by Downer (1996). Using an informative prior slightly reduced the estimated home range size, but the estimate was still higher than estimates from studies using GPS collars. It is possible that home range sizes in Peru are larger than in Colombia and Ecuador due to differences in habitat, or that the telemetry data based on a small number of individuals underestimates the average home range size at the population level, but it is also possible that we are overestimating home range size with our data due to some longer-distance movements of a few individuals, which could lead to an underestimation of density.

We improved occupancy estimates of mountain tapir at TNNS from Mena et al. (2020) by including additional surveys. Our results provide strong support that the main predictors of habitat use for this species are human disturbance and slope. Similarly, Rivero et al. (2021) found topographic heterogeneity as a main predictor of Baird's tapir occupancy in the mountains of southern Mexico. In southern Ecuador, the distribution of shrubs and grassy paramo plants was associated with both elevation and slope (Keating 1999) and variation in topographic factors such as aspect, elevation, and slope influenced vegetation composition in Andean paramos (Sklenář 2006; Peyre et al. 2018). Thus, an indirect effect of the slope on tapirs through vegetation could be expected in TNNS, but we did not have detailed enough vegetation data to directly measure the effect of vegetation on tapir occupancy. A binary paramo/forest variable was not significant, indicating that tapirs use both habitat types equally. Habitat use of lowland tapirs in Brazil increased with increasing distance to roads, a proxy related to human activity, especially hunting (Cruz et al. 2014; Ferreguetti et al. 2017). In Guyana, Hallett et al. (2019) found a significant positive correlation of lowland tapirs occupancy with increased distance to villages, similar to our results for mountain tapirs. This result is probably explained considering that throughout the buffer zone of the TNNS there are several villages, including one of them inside the protected area. All these villages have as their main activity agriculture. In fact, the preference for less disturbed areas away from human activities appears to be a general pattern for tapirs (Tobler 2002; Rivero et al. 2021).

While there are some uncertainties around our density assessments, we estimated the total population size in the Sanctuary to be between 18 and 30 adult individuals, which is too low to maintain a viable long-term population if there is no functional connectivity with other areas (Lizcano et al. 2005). Currently, there are several ongoing conservation initiatives in Peru such as regional and private conservation concessions, but more focus needs to be put on protecting the remaining habitat patches and improving connectivity among tapir populations, especially across the border between Peru and Ecuador. Furthermore, an evaluation of connectivity and an assessment of genetic diversity of mountain tapirs throughout their range, but particularly at the southern end of their distribution, is needed to improve our understanding of the conservation status of the species.

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Chapter 13
Interweaving Scientific and Local Ecological Knowledge Through Studying the Salience of Wild Mammals in Two Protected Areas in the Monte Ecoregion of Argentina

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Abstract To increase conservation effectiveness in protected areas (PA) and restore biological and cultural diversity, it becomes essential to integrate different knowledge systems. A useful conceptual tool to combine local and scientific ecological knowledge is the multidimensional concept of cognitive salience of wildlife. We studied the cognitive salience of wild mammals for people living around two PA in the Monte ecoregion of Argentina: the Ischigualasto Provincial Park (IPP) and the Ñacuñán Biosphere Reserve (ÑBR). We analyzed how the cognitive salience of species (established through a freelisting and salience index) can be explained by ecological (measured through species occupancy models) and cultural (expressed as material cultural value index under the framework of nature contributions to people) aspects of salience. The cognitive salience of species had a positive correlation with the latent occupancy of mammals but was statistically significant only in the IPP. In the ÑBR, we did not find a strong link between salience index and latent occupancy, not even for those species occupying habitats close to people, such as *Lycalopex gymnocercus*, associated with sites outside the reserve, and *Sus scrofa*, preferring habitats near roads. Nevertheless, in both protected areas, the material cultural values related to the present and past use of mammals as food, medicine, ornaments, and for skin trade were relevant to explain the salience of mammals to local people.

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13.1 Introduction

Nature and its contributions to people are vital for human existence and human well-being. However, according to the global assessment of the Intergovernmental Science-Policy Platform on Biodiversity and Ecosystem Services, both nature and nature's contributions to people, are declining faster than at any time in human history (Díaz et al. 2019). The key concept of nature's contributions to people (NCP; Díaz et al. 2015, 2018; Mastrángelo et al. 2019) recognizes the central role of culture in the relationships between nature and people, and it goes beyond that of ecosystem services by explicitly embracing other worldviews and by introducing the context-specific perspective (Pascual et al. 2017). As different human groups experience the elements of nature from different knowledge systems, NCPs may be positive (i.e., benefits) or negative (i. e. detriments or losses) depending on cultural, socioeconomic, and equity concerns (Pascual et al. 2017; Díaz et al. 2018). The NCP framework identified three broad groups of contributions, defined according to the type of contribution they make to people's well-being and with culture permeating through and across all of them: regulating, nonmaterial, and material (Díaz et al. 2018). Regulating contributions are functional and structural aspects of nature that modify environmental conditions experienced by people. For example, soil organisms that are essential for the supply of nutrients to plants. Nonmaterial contributions are nature's effects on subjective or psychological aspects underpinning people's quality of life. For instance, species or ecosystems provide opportunities for recreation and inspiration. Finally, material contributions are substances, objects, or other material elements from nature that sustain the physical existence and material assets. For example, organisms used as food, energy, or materials for ornamental purposes (Díaz et al. 2018).

In the face of biodiversity loss, the most used strategy to conserve biodiversity is the creation of protected areas. Since the creation of Yellowstone National Park in the United States in 1872, these spaces were initially destined to protect areas of great scenic beauty (Diegues 2000), following models of strict protectionism and authoritarian conservation, excluding the local people. Starting in the 1980s, community-based conservation models emerged attempting to integrate the human communities that inhabit protected natural areas (Tolón Becerra and Lastra Bravo 2008; D'Amico 2015). Currently, there is broad consensus that protected areas are not enough to ensure biodiversity conservation and will have limited prospects without the cooperation and support of local people (Wells and McShane 2004).

Given the need to recognize the role of culture in nature–people relationships, the multidimensional concept of "cognitive salience" could guide an approach that addresses both ecological and cultural concerns. The cognitive salience of a species to people depends on the individual's sensitivity, personal experience, culture, and context, among other factors, and will result in some species having higher cognitive salience than others. Salience includes all those species' characteristics (e.g., phenotypic, perceptual, ecological, and cultural traits) that explain how species capture people's attention (Hunn 1999; Gosler 2017).

On the one hand, ecological salience reflects some aspects of the species' population biology and considers that animals and plants vary in abundance along with different habitats within the territory of a human group. It has been proposed that more abundant, widely distributed, and confiding species are more likely to be noticed by humans than less abundant, less widely distributed, migratory, or secretive ones (Hunn 1999). Ecological salience also has a cultural component related, for example, to people's activities, resulting in high familiarity with some species. In this sense, ecological salience could be understood as an index of the likelihood of meaningful encounters between people and organisms as a function of the abundance and distribution of species populations (Hunn 1999). On the other hand, cultural salience denotes the importance attributed to an organism due to its role in local culture (Hunn 1999). On a continuum of increasing cultural value, some organisms are central to the physical survival of people (relevant roles in diet, materials, medicine, etc.), whereas others are culturally key species because they are crucial to the culture's survival (Cristancho and Vining 2004). Few studies have analyzed the relationship between the ecological and cultural salience of animals (e.g., Gosler 2017; Silva Neto et al. 2017; Zamudio and Hilgert 2017; Wajner et al. 2019) and, in general, ecological salience was obtained from assessments of the informants' perceptions. As far as we know, no studies have evaluated the ecological salience of animals using trail cameras and occupancy modeling.

We consider that the notion of cognitive salience is useful for interweaving different knowledge systems and putting them to work together in mutually enriching ways. In this work, we combine local and scientific ecological knowledge in the study of wild animal salience to people living around two protected areas in the Monte ecoregion of Argentina: the Ischigualasto Provincial Park and the Ñacuñán Biosphere Reserve. Thus, the main objective of our work was to analyze how the cognitive salience of local wild mammals can be explained by ecological and cultural aspects of salience. Our research questions were the following:

(a) Which wild mammals have high cognitive salience to local people? and
(b) Which wild mammals occupy more sites in areas with human presence? Occupancy by species is related to anthropic covariates, such as the protection status of areas and the presence of roads. Some species use more open and disturbed habitats, such as the Patagonian mara (*Dolichotis patagonum;* Kufner and Chambouleyron 1991; Tabeni et al. 2013; Beninato et al. 2021), whereas other elusive species use the interior areas of the reserves and stay away from the roads (Forman et al. 2003; Cappa et al. 2019; Sáenz-Bolaños et al. 2020).
(c) What is the relationship like between the cognitive salience of species and their occupancy in the studied areas? We assume that a greater probability of encounters between people and mammals increases cognitive salience because immediateness is an important variable generating the link with species. The species that occupy the anthropized areas (areas of influence or edges of the protected

areas, roads) have a high probability of encountering people, and thus, these mammals will have a high cognitive salience to them.

(d) What wild mammals are more culturally important based on the material NCP category? The cultural importance of species could be estimated in part by quantifying their material value (Tamburini et al. 2021). Thus, some species preferred for consumption, such as the armadillos, will be more important regardless of their occupancy.

(e) Is the cultural material value of species related to cognitive salience? Even though the salience of animals would reflect not only their material or utilitarian importance but also complementary perceptions, such as animal–human conflicts, as well as nonmaterial values (Gosler 2017; Hunn 1999; Wajner et al. 2019; Campos et al. 2021; Tamburini et al. 2021), we expected a strong correlation between cultural material value and cognitive salience.

13.2 Methods

13.2.1 Study Localities

The research was conducted in two protected areas: the Ischigualasto Provincial Park (IPP) and its area of influence (29° 55′ S, 68° 05′ W, San Juan Province, Fig. 13.1), and the Ñacuñán Biosphere Reserve (ÑBR) including its population and a neighboring cattle field (340° 02′ S, 670° 58′ W, Mendoza Province, Fig. 13.1). The IPP is located in the Monte of hills and closed basins ecoregion (Fig. 13.2) and it extends over 62,916 ha. Mammals are represented by 22 species (Giaccardi et al. 2015), some of them vulnerable, such as mountain viscacha rat (*Octomys mimax*), *D. patagonum*, and collared peccary (*Pecari tajacu*) (Alonso Roldán et al. 2019; Campos 2019; Camino et al. 2019; Ontiveros et al. 2020). Also, exotic species occur in the park: European hare (*Lepus europaeus*), donkey (*Equus africanus asinus*), horse (*Equus ferus caballus),* mule (*Equus mulus*), and cattle (*Bos primigenius taurus*) (Giaccardi et al. 2015). Historically, since the late nineteenth and early twentieth centuries, the area constituted an important route associated with the transport and trade of cattle. Since the 1930s, local people from the villages have worked as miners and as local guides for scientific expeditions in search of fossil remains (Jofré 2008). The IPP was created in 1971 to preserve the paleontological wealth of the site for scientific study. In 2000, together with the Talampaya National Park, the IPP was incorporated into the World Heritage Sites.

The research was conducted in a southern portion of the IPP, covering approximately 15,000 ha between the park ranger’s house and the closest locality (Los Baldecitos). Interviews were conducted with the people of Los Baldecitos, a village of 60 inhabitants located 9 km from the entrance to the IPP (Fig. 13.1). Currently, people live mainly on retirement income, state jobs, tourism, and cattle raising (Jofré 2008). The latter is in decline due to issues related to land ownership, shortage of

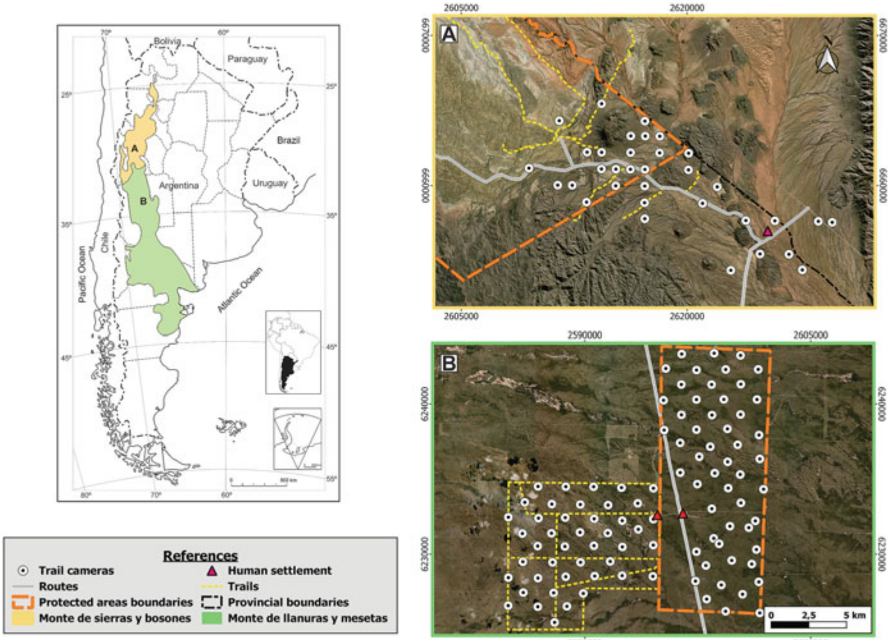

Fig. 13.1 Study sites as representative of two areas of the Monte ecoregion: (**a**) Monte of hills and closed basins (Ischigualasto Provincial Park); (**b**) Monte of plains and plateau (Ñacuñán Biosphere Reserve)

young people for the required duties, predation of carnivores on domestic animals, and restrictions in the protected area.

The ÑBR is located in the Monte of plains and plateau (Fig. 13.2) and it encompasses 12,800 ha. It is the only fenced protected area in the Monte, surrounded by cattle fields. The reserve is free from livestock since 1972, with a remarkable passive recovery of the native flora (Ojeda et al. 1998). Mammals are represented by 31 species (Cuello et al. 2016), and some of them are threatened: Pampas cat (*Leopardus pajeros*), *D. patagonum*, and *P. tajacu* (Alonso Roldán et al. 2019; Camino et al. 2019; Lucherini et al. 2019). Two exotic mammals occur inside the protected area: *L. europaeus* and wild boar (*Sus scrofa*). The ÑBR was created in 1961 to protect the relicts of native forests (*Neltuma flexuosa*) that had remained after the intensive logging carried out until the second third of the twentieth century. Later, in line with global trends, the reserve was included in the UNESCO network of Man and Biosphere Reserves (1986).

On the edge of the reserve and close to the route is the locality of Ñacuñán, currently inhabited by around 80 people (Fig. 13.1). The economically active population are public employees, employees of the livestock sector and people dedicated to commerce (Torres et al. 2010). This Creole population that historically settled in the locality was associated with the railway and the intensive use of native

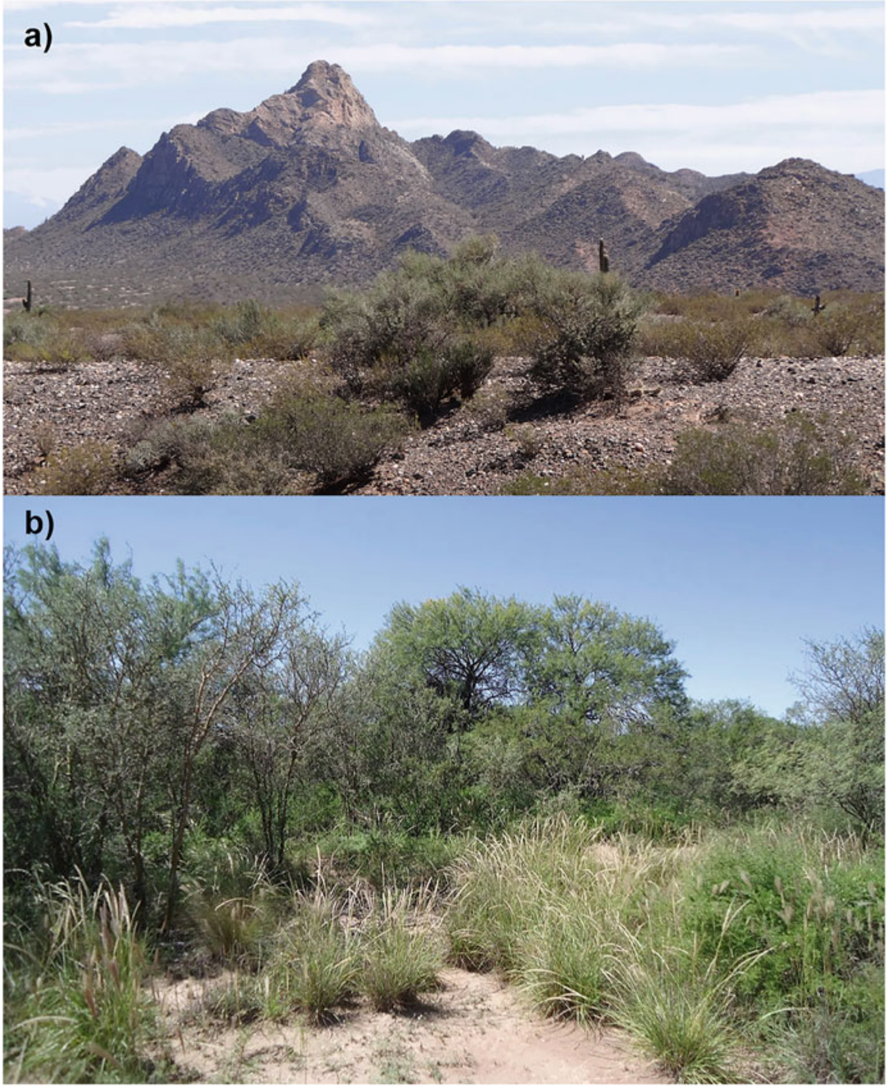

Fig. 13.2 (**a**) Ischigualasto Provincial Park (San Juan, Argentina), (**b**) Ñacuñán Biosphere Reserve (Mendoza, Argentina), and influence area of the reserves. Trail camera stations and habitats most used by local people are shown: human settlements (Los Baldecitos and Ñacuñán), and roads (trails and routes)

forests, at the beginning of the twentieth century (Abraham 2001). The provincial administrations (Direction of Conservation and Protected Areas of San Juan and Direction of Renewable Natural Resources of Mendoza) fully authorized this research in the protected areas.

13.2.2 Cognitive Salience of Species to People

Freelisting is a collection technique extremely useful for a rapid survey of people's knowledge (Brewer 2002). It has been widely applied and has proven to generate important knowledge in ethnobiological studies (Quinlan 2019). Freelisting rests on three assumptions: people tend to list terms in order of familiarity; individuals who know a lot of species list more terms than people who know less, and terms that most people mention indicate locally salient items (Quinlan 2019). However, this technique has some limitations. For example, it was found that people have a temporal cognitive limit on the retrieval of knowledge, because individuals tend to recall information about species used during the preceding year (Sousa et al. 2016). The leading question of the free lists was "What wild animals can you see in this area?" (Brewer 2002; Albuquerque et al. 2014). Species identification was confirmed using pictures from guidebooks on animals and photos taken in the study area. We engaged 20 informants in freelisting interviews in Los Baldecitos, and 28 informants in Ñacuñán, covering at least one informant (older than 18 years old) per household. Of all species mentioned by people, we focused on terrestrial mammals because they are the species best detected by camera traps, and this allowed us to compare the results obtained by social methodologies with those obtained by ecological methodologies.

We estimated the cognitive salience index (Sutrop 2001) to quantify the perceived relative importance of mammals named in the resulting free lists. We included the items mentioned at least twice by the informants. The index takes into account the item's frequency, its mean position, and the number of informants. It is free from the side effects caused by the length of lists. The formula is: $S = F^2/(N\,\Sigma\, R_j)$, where F is an item's frequency (number of lists where an item is named), N is the total number of informants, and R is the rank of an item in each list (j) (Sutrop 2001). The salience index varies between 0 (the least salient items) and 1 (the most salient items). As members of the Latin American Society of Ethnobiology (SOLAE), we followed the Code of Ethics guidelines (SOLAE Ethics Committee et al. 2018). From the beginning, the purpose of our study was explained to the informants, and their free prior and informed consent were obtained.

13.2.3 Ecological Aspects of Salience: Occupancy by Mammals

We estimated occupancy for the species using trail cameras. Occupancy is a state variable of animal occurrence and can be defined as the proportion of sites occupied by a species (Rovero and Zimmermann 2016). We installed 50 trail camera stations in the IPP and 100 in ÑBR and their influence areas, within a $1 \times 1\ \text{km}^2$ regular grid (Fig. 13.1). Samplings were done between February and March 2019 in the IPP and from November 2017 to June 2018 in the ÑBR. We set up 50 trail cameras

(40 Moultrie 999i and 10 Primos Truth Cam46) in IPP and 30 cameras (Moultrie 999i) in the ÑRB which were rotated among the sampling stations, being relocated every 30 days. Cameras were mounted on metal stakes at 40 cm height and operated 24 h per day. We measured detection distance (D dist) as the maximum distance (m) at which the camera can capture passing-by animals. Cameras were set to take three consecutive photos with a 30 s delay. Photo series from the same trail camera for the same species were considered independent when individuals could be differentiated or if 30 minutes passed with no captures of the respective species. To analyze the trail camera data, we only considered cameras with at least 15 functioning days. Based on camera-trap surveys, we generated detection histories for each locality and species. Detection histories are matrices with binary values of 1 denoting detection and 0 for nondetection, specific to each camera station across different sampling occasions (MacKenzie et al. 2018). We defined a site as a single-camera-trap station. Different sampling occasions were selected for each species, considering the compromise between the model fit and an adequate number of visits, accepting a minimum of two occasions.

For each study locality, we built single-species single-season occupancy models with a likelihood-based approach to estimate probabilities of site occupancy (*psi*) and detection (*p*) for wild species as a function of the covariates (MacKenzie et al. 2018). Models were fitted using a logit link function. We selected candidate models following a two-step approach. In the first step, we built models with occupancy held constant and detection as a function of distance to the closest obstacle from the camera (D dist). We used the camera model (C mod) combined with an additive model with both variables (D dist + C mod) for IPP models, whereas in ÑBR we used only D dist. In the second step, we used the selected model from detection probability (first step) and we model occupancy as a function of different covariates: inside or outside the reserve (Res), type of road (R type), distance to the nearest road (R dist), and an additive model combining the last two (R type + R dist). All numerical covariates were standardized by z-score prior to analysis. Then, we calculated the Variance Inflation Factor (VIF) to visualize whether there was collinearity among all covariates (Heiberger and Holland 2004), but we did not find it.

To rank the candidate models, we used the corrected Akaike Information Criterion by small sample sizes (AICc) (Burnham and Anderson 2010). Models with a value of ΔAIC <2 were selected as top models in each step. In cases where the most complex model showed an over-dispersal parameter of c-hat >1 and <4, we used the second-order quasi-Akaike Information Criterion (QAICc) corrected by the c-hat to select the models (MacKenzie and Bailey 2004; Burnham and Anderson 2010). If the value of c-hat was >4 we made a ranking with the most complex models using four values of c-hat: 1, 2, 3, and 4. Because the ranking did not show any change in the order of models, we interpreted the results using the higher value of c-hat (c-hat $= 4$) and the QAICc. When the value of c-hat was lower than one, we ignored this under-dispersal since results were not affected (Burnham and Anderson 2010). When we obtained similar candidate models with a small QAICc difference (ΔQAICc <2) and with no single model having an Akaike weight >0.90, we chose the most parsimonious model (i.e., fewer parameters, Burnham and Anderson

2010) to estimate latent occupancy. The direction and magnitude of covariate effects were based on selected model estimates (Burnham and Anderson 2010).

Finally, ecological salience was defined as the number of sites occupied by each species (latent occupancy). Latent occupancy was estimated with the best model for each species using the empirical Bayes method available in the *ranef* function, in *unmarked* package (Fiske and Chandler 2011). All analyses were performed in R version 3.6.1 (R Core Team 2016) using the *camtrapR* (Niedballa et al. 2016) and *unmarked* packages (Fiske and Candler 2011).

13.2.4 Cultural Aspect of Salience: The Material Nature's Contributions to People

Field notes and 45 semistructured open interviews ($N = 15$ informants in Los Baldecitos, $N = 30$ informants in Ñacuñán) were conducted between 2017 and 2019 (Hernández Sampieri et al. 2010; Albuquerque et al. 2014). The informants were mostly people who responded to the questionnaires and expressed interest in talking in greater depth about the species. We inquired regarding the use of species in the past and present because some material contributions that were profitable or beneficial in the past are currently not active in the context of protected area regulations. In addition, all relevant information arising during the freelisting task was considered.

For the analysis, we digitized the interviews and field notes and made a qualitative analysis, first identifying the fragments with topics of interest, then carrying out a first-level grouping where meanings were assigned to the highlighted fragments. Finally, a second level was assigned grouping that referred to higher levels of abstraction and conceptualization (Flores-Kanter and Medrano 2019). In this last step, the material NCP mentioned by people were taken into consideration, following the categories recommended by IPBES (Díaz et al. 2018): food and feed (NCP 12), materials, companionship, and labor (NCP 13), and medicinal resources (NCP 14).

We calculated the Material Cultural Value (MCV) of each mammal species following the index proposed by Reyes-García et al. (2006) and including the approach of Tamburini et al. (2021): $\mathrm{MCVe} = \mathrm{Uce} * \mathrm{Ice} * \Sigma \mathrm{IUce}$, where MCVe is the material cultural value of species *e*, Uce is the total number of material NCP categories reported for the species *e* divided by the potential material NCP categories considered in this study, Ice expresses the number of interviews who named the species *e* divided by the total number of participating people, and lUce indicates the number of participants who mentioned each material NCP of the species *e* divided by the total number of participants. The magnitude of the MCV index reflects the cultural importance of a species from the perspective of people.

13.2.5 *Correlation of Salience Index with Latent Occupancy and Material Cultural Value*

We analyzed the relationships between the salience index with latent occupancy and the MCV index for each species. For the first correlation, we used the estimated latent occupancy, which represents the total number of occupied sites estimated based on occupancy probability. In the cases where occupancy models did not converge, we considered the number of sites where species were recorded by trail cameras as a proxy of latent occupancy.

In the correlation analyses, we included all mammals listed by people. We tested the normality of distribution using the Shapiro–Wilk test (salience index: $W = 0.76$, p-value $= 0.0001$; occupancy estimates: $W = 0.80$, p-value $= 0.0001$; MCV index: $W = 0.71$, p-value $= 0.0001$) and, due to the lack of normality, we used the Spearman correlation coefficient. Correlation analyses were performed in R using the *ggpubr* package (Kassambara 2020).

13.3 Results

13.3.1 *Cognitive Salience of Species to People*

We interviewed 20 informants (45% women and 55% men) in Los Baldecitos, mostly elderly people (mean = 54.7 years old, SE = 15.1), and 28 informants (54% women and 46% men) in Ñacuñán (mean = 50.4 years old, SE = 18.1). There was no species-level correspondence between the local names (ethnospecies) provided in freelisting interviews and the scientific names of species recorded by trail cameras. We found underdifferentiation in ethnospecies because some local names were applied to a genus or unrelated species. Using the single name "armadillos," people alluded to a group of three species: *Zaedyus pichyi*, *Chaetophractus vellerosus,* and *C. villosus*. *Galictis cuja* and *Lyncodon patagonicus* were both named "hurones." The informants mentioned, at least twice, a total of 13 ethnospecies in the IPP and 14 in the ÑBR (Table 13.1). Eleven species were mentioned by local people of both study sites, and *D. patagonum* (Fig. 13.3) was the species with the highest salience to people. *Lama guanicoe* (Fig. 13.3) and *Lagidium viscacia* occur only in the IPP, whereas hurones, *L. pajeros* and *Herpailurus yagouaroundi* (Fig. 13.4), were exclusively mentioned in the ÑBR (Table 13.1).

13.3.2 *Ecological Aspects of Salience*

Some cameras stopped functioning and some others were displaced by animals with the consequent loss of days of camera operation; thus, we considered records from

Table 13.1 Cognitive salience of mammals to people in the IPP (Ischigualasto Provincial Park) and in the ÑBR (Ñacuñán Biosphere Reserve)

Scientific name	Common local name	Order, family	Salience Index	
			IPP	ÑBR
Dolichotis patagonum	liebre, liebre criolla, mara	Rodentia, Caviidae	0.33	0.27
Lama guanicoe	guanaco	Cetartiodactyla, Camelidae	0.18	–
Lepus europaeus	liebre japonesa, liebre orejuda, liebre europea, liebre de Castilla	Lagomorpha, Leporidae	0.15	0.04
Armadillos (*Zaedyus pichiy, Chaetophractus vellerosus* and *C. villosus)*	armadillos (piche o quirquincho blanco, mulita, quirquincho negro o peludo respectively)	Cingulata, Chlamyphoridae	0.12	0.14
Puma concolor	león, puma	Carnivora, Felidae	0.05	0.11
Lycalopex gymnocercus	zorro	Carnivora, Canidae	0.10	0.09
Sus scrofa	jabalí, chancho jabalí	Artiodactyla, Suidae	0.02	0.08
Conepatus chinga	zorrino, chiñe	Carnivora, Mephitidae	0.06	0.04
Microcavia maenas	conejo, conejito del cerco	Rodentia, Caviidae	0.03	0.06
Lagostomus maximus	vizcacha, vizcacha leñatera	Rodentia, Caviidae	0.02	0.04
Lagidium viscacia	vizcacha de la sierra	Rodentia, Chinchillidae	0.03	–
Pecari tajacu	pecarí, chancho del monte, chancho pecarí	Artiodactyla, Tayassuidae	0.03	0.02
Leopardus geoffroyi	gato montés	Carnivora, Felidae	0.02	0.03
Hurones (*Galictis cuja* and *Lyncodon patagonicus*)	hurón	Carnivora, Mustelidae	–	0.03
Leopardus pajeros	gato del pajonal	Carnivora, Felidae	–	0.02
Herpailurus yagouaroundi	gato del agua, gato colorado	Carnivora, Felidae	–	0.01

Scientific names, common names, and salience index are shown. Salience index was obtained by free listing ($N = 20$ informants in the IPP; $N = 28$ in the ÑBR)

34 cameras in IPP and 94 in ÑBR. The average number of camera days for a camera across the study period was 28 (IPP) and 27 (ÑBR). The total sampling nights were 955 for IPP and 2543 for ÑBR.

We obtained independent records of 22 wild mammal species, with two of them being exotic (*L. europaeus* and *S. scrofa*). In the cases when cognitive salience was calculated, we tried to fit occupancy models to obtain the latent occupancy data. In

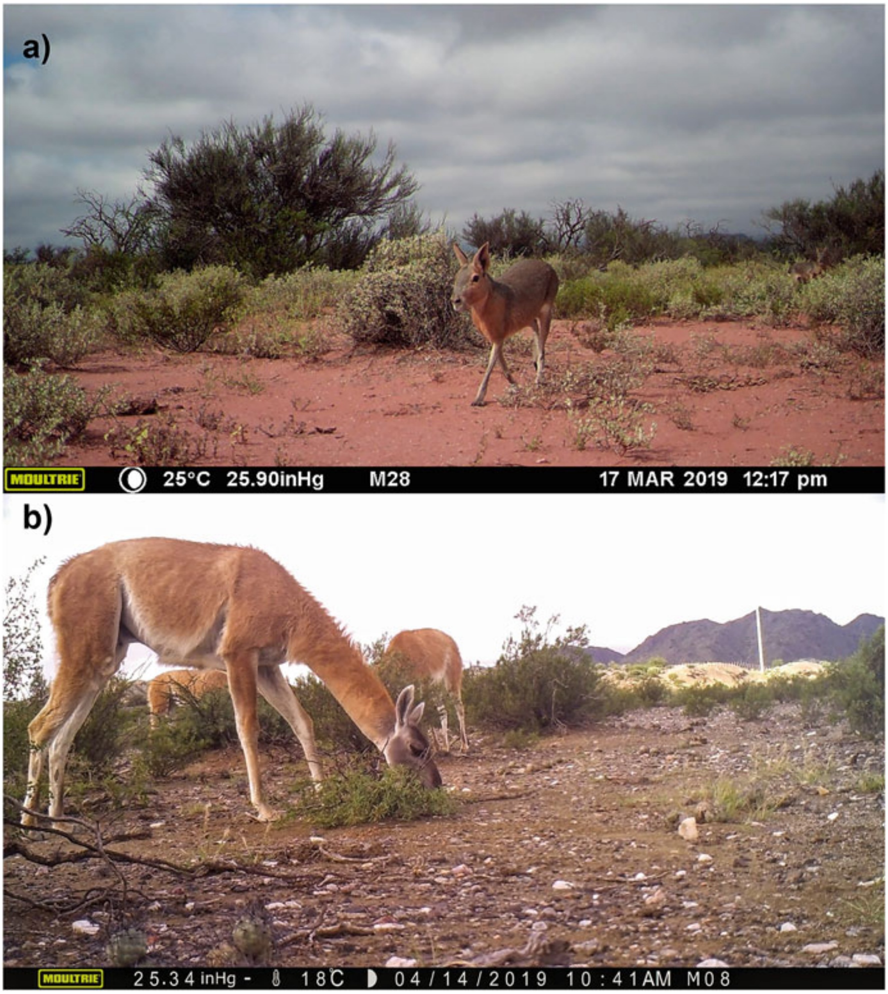

Fig. 13.3 Examples of mammals captured by trail cameras and mentioned by local people in the Ischigualasto Provincial Park. (**a**) *Dolichotis patagonum*; (**b**) *Lama guanicoe*

general, the selected covariates were unable to explain the occupancy by species. For three species in the IPP and five in the ÑBR, the null model was the best model (Table 13.2). For the remaining cases, at least one covariate affected the occupancy probability or the detection probability (Table 13.2). In the IPP, latent occupancy was higher for *L. gymnocercus*, followed in descending order by *D. patagonum,* and *C. chinga*. In the ÑBR, *M. maenas* was the species that occupied more sites, followed by *L. gymnocercus* and *L. geoffroyi* (Table 13.2). We were able to identify mammals that were more or less associated with the protected areas. For *L. guanicoe* in the IPP and *L. geoffroyi* in the ÑBR, latent occupancy was higher inside the protected areas, whereas *D. patagonum* and *L. gymnocercus* occupancy was higher

Fig. 13.4 Examples of mammals captured by trail cameras and mentioned by local people in the Ñacuñán Biosphere Reserve. (**a**) *Leopardus pajeros*; (**b**) *Herpailurus yagouaroundi*

outside the ÑBR. Regarding the distance to roads, only occupancy by the exotic *S. scrofa* was higher near roads (Table 13.2).

13.3.3 Cultural Aspects of Salience

In the IPP, *L guanicoe*, *D. patagonum*, armadillos, *P. concolor*, and *L. gymnocercus* were the ethnospecies with the highest MCV index (Table 13.3). In the ÑBR, they were *D. patagonum*, armadillos, *P. concolor*, and *S. scrofa* (Table 13.3). Overall, the

Table 13.2 Species-specific occupancy values (*psi*) and detection probability (*p*) estimations for species mentioned at the study areas: Ischigualasto Provincial Park (IPP) and Ñacuñán Biosphere Reserve (ÑBR)

Species	Site	*Naïve occupancy*	*Days / occasion*	*p*	SE *p*	*psi*	SE psi	*p C* mod [models]	*p* D dist	*psi* Res [situations]	*psi* R dist	c-hat	Latent *occupancy*
Dolichotis patagonum	IPP	64.71	5	0.40	0.05	0.70	0.09					1.04	23.49
Lama guanicoe	IPP	52.94	6	0.36	0.06	0.35	0.15			+[inside]		0.98	21
Lepus europaeus	IPP	35.29	6	0.29	0.11	0.56	0.20					1	20
Armadillos *(Zaedyus pichiy, Chaetophractus vellerosus* and *C. villosus)*	IPP	11.76											4^{a}
Lycalopex gymnocercus	IPP	88.24	4	0.41	0.04	0.97	0.05	– [primos]				1.15	33.13
Conepatus chinga	IPP	32.35	7	0.14	0.09	0.68	0.38					2.12	23
Puma concolor	IPP	5.88											2^{a}
Microcavia maenas	IPP	0											0^{a}
Lagidium viscacia	IPP	0											0^{a}
Pecari tajacu	IPP	5.88											2^{a}
Leopardus geoffroyi	IPP	11.76											4^{a}
Lagostomus maximus	IPP	0											0^{a}
Sus scrofa	IPP	0											0^{a}
Dolichotis patagonum	ÑBR	17.05	5	0.37	0.05	0.42	0.08			−[inside]		1.74	17.5
Armadillos *(Zaedyus pichiy, Chaetophractus vellerosus* and *C. villosus)*	ÑBR	35.11	8	0.33	0.06	0.42	0.08					2.18	39.52
Puma concolor	ÑBR	15.96	7	0.24	0.08	0.24	0.08					0.39	22.45
Lycalopex gymnocercus	ÑBR	82.98	7	0.76	0.03	0.97	0.03		+	−[inside]		>4	76.38
Sus scrofa	ÑBR	22.36	8	0.13	0.05	0.57	0.19		+		(−)	0.18	53.77
Microcavia maenas	ÑBR	82.98	8	0.77	0.03	0.84	0.04					>4	79.29

Lagostomus maximus	ÑBR	0											0[a]
Conepatus chinga	ÑBR	36.17	8	0.26	0.05	0.57	0.12					2.03	53.60
Lepus europaeus	ÑBR	1.06											1[a]
Hurones (*Galictis cuja* and *Lyncodon patagonicus*)	ÑBR	11.70											11[a]
Leopardus geoffroyi	ÑBR	64.89	8	0.43	0.04	0.62	0.1			+[inside]		1.08	73.7
Pecari tajacu	ÑBR	5.32	8	0.33	0.17	0.08	0.04					0.03	5
Leopardus pajeros	ÑBR	5.32											5[a]
Herpailurus yagouaroundi	ÑBR	4.26											4[a]

Covariates that appear in the best models, directionality (+/−) and brackets when their confidence intervals included the zero value are shown

psi occupancy probability, *p* detection probability, *C mod* camera model (MULTRIE and PRIMOS), *D dist* detection distance (m), *Res* conservation status (outside or inside the reserve), *R dist* road distance (m), *c-hat* overdispersion value, Latent occupancy estimated

[a] number of sites where the species were recorded; occupancy models did not converge for these species

Table 13.3 Material nature's contributions (NCP) to people and Material Cultural Value index for mammals in the IPP (Ischigualasto Provincial Park) and in the ÑBR (Ñacuñán Biosphere Reserve)

Scientific name	Food and feed		Materials, companionship, and labor		Medicinal resources		MCV	
	IPP	ÑBR	IPP	ÑBR	IPP	ÑBR	IPP	ÑBR
Lama guanicoe	7	–	3	–	2	–	0.54	–
Dolichotis patagonum	8	19	3	4	0	1	0.32	0.51
Armadillos *(Zaedyus pichiy, Chaetophractus vellerosus* and *C. villosus*)	9	17	1	2	0	1	0.26	0.47
Puma concolor	3	7	2	6	2	9	0.22	0.43
Sus scrofa	2	14	0	2	0	0	0.001	0.20
Lycalopex gymnocercus	2	0	4	10	0	0	0.15	0.07
Conepatus chinga	0	1	1	1	0	1	0.01	0.04
Lagostomus maximus	4	6	0	0	0	0	0.02	0.02
Lepus europaeus	2	1	0	0	0	0	0.02	0.001
Leopardus geoffroyi	0	0	1	6	0	0	0.001	0.02
Pecari tajacu	2	4	0	0	0	0	0.01	0.01
Lagidium viscacia	2	–	0	–	0	–	0.01	–
Leopardus pajeros	0	0	0	2	0	0	0	0.001
Herpailurus yagouaroundi	0	0	0	2	0	0	0	0.001
Microcavia maenas	0	0	0	0	0	0	0	0
Hurones (*Galictis cuja* and *Lyncodon patagonicus*)	0	0	0	0	0	0	0	0

Frequency of mentions by locality. *MCV* material cultural value index

most important mammalian NCP was linked to food provision. The meat of some species is well known for its use as food, such as that of *L. guanicoe* (as beef and as salt-cured meat), *D. patagonum*, armadillos, *L. europaeus*, *L. viscacia*, *L. maximus, S. scrofa* and *Pecari tajacu*. The use for consumption by humans and domestic animals (dogs) was mentioned for *P. concolor* and *L. gymnocercus*. However, hunting of these animals is not directly related to obtaining food, but rather to the conflict generated by tangible damages caused to people due to predation of *P. concolor* and *L. gymnocercus* on domestic animals (chicken, goats, foals, and calves). However, the local people mention that at present they do not capture many animals because of the prohibitions in protected areas.

Although currently skins have no commercial value, people mentioned the past commercial use of skins of *L. gymnocercus*, *C. chinga*, *P. concolor*, *L. geoffroyi* (in both protected areas), and *L. pajeros* and *H. yagouaroundi* (in the ÑBR). The body parts of some species were mentioned for making crafts, for instance, the leather strips of *D. patagonum* for sewing cowhide, the shell of armadillos, the head of *S. scrofa* for making crafts, the skin of *P. concolor* for making ornaments and its hunting nail as a trophy and the wool of *L. guanicoe* was mentioned as used in the past.

Some body parts of mammalian species were also mentioned for their use as medicinal resources. The fat of *P. concolor* was mentioned for both protected areas. The leg and marrow of *L. guanicoe* were cited for the IPP, the fat of C. *chinga* and armadillos, as well as the leg of *D. patagonum* for the ÑBR. The use as pets of *D. patagonum*, *L. gymnocercus*, S. *scrofa*, and armadillos was cited for both study sites. Local people did not mention any material use for *Microcavia maenas* or hurones (Table 13.3).

13.3.4 Correlation of Salience Index with Latent Occupancy and Material Cultural Value

Some mammals mentioned by local people were not recorded by trail cameras (*M. maenas, L. viscacia, L. maximus,* and *S. scrofa* in the IPP; *L. maximus* in the ÑBR). Mentions of some species (such as *Ctenomys mendocinus*, *Graomys griseoflavus*, *O. mimax*, and *Chlamyphorus truncatus)* were not considered in the subsequent analyses because the study of habitat occupancy by these species requires the application of different sampling designs (i.e., capture with live traps or specific location for trail cameras). In the IPP, the relationship between salience index and latent occupancy by mammals showed a positive trend (Fig. 13.5), and a statistically significant association (Spearman $r^2 = 0.76$, $S = 88.42$, p-value $= 0.003$). Some species moved away from the correlation line, such as *L. gymnocercus*, *C. chinga* and armadillos (Fig. 13.5). In the ÑBR, there is a positive and nonstatistically significant correlation between salience index and latent occupancy by mammals (Spearman $r^2 = 0.44$, $S = 253.45$, p-value $= 0.11$; Fig. 13.5).

In the IPP, the relationship between the salience index and MCV index showed a strong positive trend, and a statistically significant correlation (Spearman $r^2 = 0.81$, $S = 69.92$, p-value $= 0.0008$; Fig. 13.6). Some species moved away from the

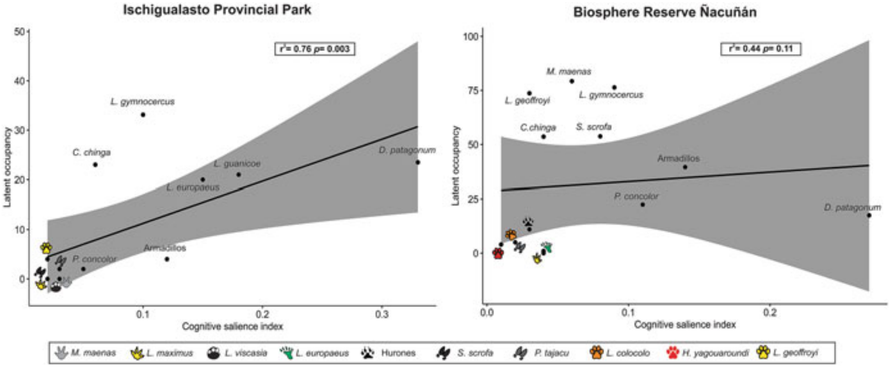

Fig. 13.5 Relationship between cognitive salience index and latent occupancy of mammals in the Ischigualasto Provincial Park and the Ñacuñán Biosphere Reserve. Spearman's r^2 and p are shown

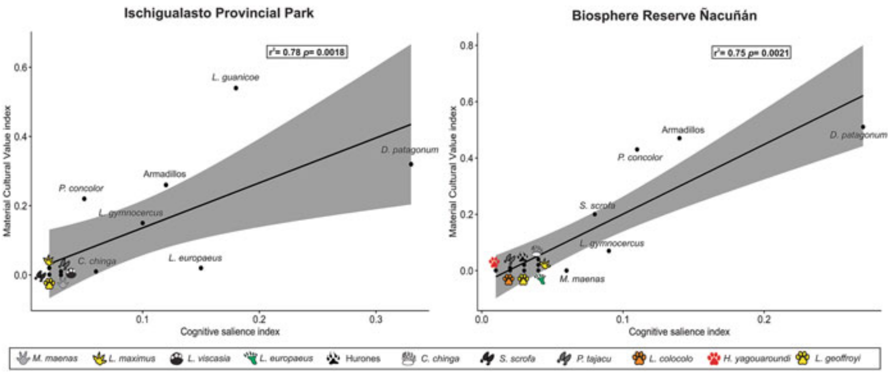

Fig. 13.6 Relationship between cognitive salience index and material cultural value of mammals in the Ischigualasto Provincial Park and the Ñacuñán Biosphere Reserve. Spearman's r^2 and p are shown

correlation line, such as *L. guanicoe,* armadillos and *P. concolor* because they had a higher MCV than expected (Fig. 13.6). In the ÑBR, there was a strong, positive, and statistically significant correlation between salience index and MCV index (Spearman $r^2 = 0.75$, $S = 114.51$, p-value $= 0.002$; Fig. 13.6). *Puma concolor* and armadillos moved away from the correlation, having a higher MCV than expected (Fig. 13.6).

13.4 Discussion

Our chapter shows a way to integrate studies on the cognitive salience of species obtained through free listings, ecological studies of mammal occupancy, and cultural values recovered from interviews under the framework of NCP and including a context-specific perspective. The work brings scientific and local ecological knowledge into dialogue in the context of protected natural areas, which since their creation represent spaces with restrictions for the use of natural resources, including wildlife (Cruz and Courtalón 2017; Tamburini and Cáceres 2017; Abukari and Mwalyosi 2020). The changes that occurred in people's activities and the management of protected areas allow for changes in species occupancy, in the contributions of wild mammals to people, and in species salience.

In both protected areas, the material cultural component was relevant to explain the cognitive salience of mammals to local people. Nevertheless, the cognitive salience of species had a positive correlation with the ecological aspect of salience, represented by mammal latent occupancy, but it was only statistically significant in the IPP. We think that the lack of significant correlation in ÑBR could be explained by a higher-than-expected latent occupancy for some species (*M. maenas*, *L. gymnocercus*, and *L. geoffroyi*). In this particular area, our study was coincident with a period of atypical high precipitation (714.5 mm) in comparison with the mean annual precipitation of the last 39 years (1973–2017: 344.27 mm) (Sánchez Dómina et al. 2020). It is known that, in drylands, the increase in water availability triggers an increment in primary productivity and consequently in the populations of small herbivorous mammals and their predators (Noy-Meir 1973). We think that in our system, *M. maenas*, *L. gymnocercus*, and *L. geoffroyi* could be responding to the precipitation increase with high latent occupancy. This change in the ecological aspect of salience was probably not perceived by local people at the time we applied free listing and interviews, and therefore may not be immediately reflected in high cognitive salience for these species.

In both protected areas, the species with the highest salience to local people was *D. patagonum*, a medium-sized rodent (7–9 kg) that occupied more sites outside the ÑBR. Previous studies found that across its geographical range in drylands, this species might benefit from open habitats, where its predator detection efficiency increases (Campos et al. 2001). In the Monte, *D. patagonum* has a preferential use of open sites with cattle activity (Tabeni et al. 2013) and has represented over time a food resource for local people (Schobinger 2004; Vilela et al. 2009). Added to its high MCV, this species has a strong acceptance and is assigned the "criolla" identity, which is shared with Argentinian rural people (Campos et al. 2021). The high cognitive salience of *D. patagonum* to local people is based on their sharing the use of space and on its having a high cultural value linked to material and nonmaterial contributions to people.

The species with intermediate cognitive salience in the IPP were *L. guanicoe*, *L. europaeus,* and armadillos, while in the ÑBR they were *L. gymnocercus*, armadillos, and *P. concolor*. *Lama guanicoe* has a high occupancy in the IPP, occurring more in habitats inside the protected area, as was found in a previous study (Cappa et al. 2017). This species tends to avoid rural settlements as a response to human pressure and the presence of domestic animals (Baldi et al. 2004; Acebes et al. 2012; Schroeder et al. 2014). According to this, it has been found that there exists temporal segregation between cattle and *L. guanicoe*, particularly in areas close to roads (Cappa et al. 2019). But, although it does not frequent spaces close to people, *L. guanicoe* is a conspicuous species, with a high MCV which increases its cognitive salience. Local people mentioned the consumption of its meat, and medicinal use of its body parts, as was reported by previous studies (Vilela et al. 2009; Hernández et al. 2015). Also, the fiber of wild *L. guanicoe* is highly appreciated and represents an important resource for local people in drylands (Vilela et al. 2009). To reconcile conservation and poverty alleviation in rural areas, a feasible option for sustainable use of *L. guanicoe* seems to be live shearing, especially when the beneficiaries of animal use are low-income producers (Lichtenstein and Carmanchai 2014; Hernández et al. 2015). The exotic *L. europaeus* has high occupancy in the IPP, which seems to explain its salience to people. Its low MCV was related only to food provision, although the local people clarified that *L. europaeus* provides less meat than *D. patagonum*. In the ÑBR, the salience of *L. europaeus* was low, as well as its latent occupancy and its MCV.

The armadillos group had lower latent occupancy in the IPP than in the ÑBR. Nevertheless, its MCV was high at both study sites. Armadillos are an important food resource for indigenous and rural communities (Trillo et al. 2016; Rodrigues et al. 2020). Added to this, the species in this group have medicinal importance and are also used as ornamental resources (Rodrigues et al. 2020).

The two carnivores, *L. gymnocercus* and *P. concolor*, have intermediate cognitive salience to people. The first one had high latent occupancy at both study sites and, in the ÑBR, occupied more habitats outside the protected area. The second one was more frequently recorded in the ÑBR, although we did not detect the effect of the covariates analyzed. Both species have high MCV in the IPP, and *P. concolor* in the ÑBR, mainly related to the provision of materials. In the past, they were persecuted, because Argentina was one of the world's leading exporters of wildlife through legal and illegal trade (Mares and Ojeda 1984). The skin of wild mammals like *L. gymnocercus*, *P. concolor, L. geoffroyi, L. pajeros, G. cuja, L. patagonicus,* and *C. chinga* was employed to manufacture coats and leather accessories (Gruss and Waller 1988). Thus, the MCV of these species was related to the past and the monetary value of their skin, although at present some of them (*L. geoffroyi, L. pajeros, G. cuja, L. patagonicus* and *C. chinga*) have low cognitive salience to local people. The only record we had of *H. yagouaroundi* was in the ÑBR and *L. geoffroyi* occupied more sites inside than outside the reserve. Although at the present *L. gymnocercus* and *P. concolor* are not hunted for their skin, they are frequently slaughtered in retaliation for their predation on domestic animals (Lucherini et al. 2008; Quiroga et al. 2016; Camino et al. 2018) and, on these occasions, the people use the fat as medicine, the meat as food for themselves or their dogs, and other parts of the animal body for ornaments. In the ÑBR, the exotic *S. scrofa* had an intermediate salience to people and a high latent occupancy related to the presence of roads. Finding animals and their signs of activity is common for the local people, who hunt *S. scrofa* mainly for food supply.

Pecari tajacu, L. maximus, L. viscasia, and *M. maenas* were species with low salience to people. *Pecari tajacu* had a few records in both protected areas, but *L. maximus* and *L. viscasia* were not recorded by trail cameras. On the contrary, *M. maenas* was the species with the highest latent occupancy in the ÑBR. *Pecari tajacu, L. maximus*, and *L. viscacia* had an MCV related to their use as food. In the case of *M. maenas*, it was not assigned any MCV; thus, its salience could be related to animal abundance and nonmaterial value.

13.5 Conclusions

Conservation initiatives that take into account the social and cultural aspects of biodiversity use may benefit especially from identifying and focusing on species relevant to local people. The study of ecological local knowledge surrounding species can bring ecologists and conservation biologists a better understanding of and respect for local knowledge systems (Garibaldi and Turner 2004).

The shortage of analytical approaches focused on how different human societies create and assign values to biodiversity, and on how culture permeates nature's contributions to people, was identified as a knowledge gap by international assessments (Mastrángelo et al. 2019). Our study shows a way to interweave the ecological local and scientific knowledge to understand the relationships between people and wild mammals in a specific context of protected areas.

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Chapter 14
Occupancy Modeling Reveals That Landscape Scale Drives Habitat Use by White-Tailed Deer in the Tehuacán-Cuicatlán Biosphere Reserve, Mexico

Salvador Mandujano, Gabriel P. Andrade-Ponce, Arturo Zavaleta, and Concepción López-Téllez

Abstract The animal–habitat relationships tend to manifest at specific spatial scales and are crucial for linking habitat selection patterns to ecological processes. The white-tailed deer *Odocoileus virginianus* is a species with a wide geographical distribution, and it is used both for subsistence and game hunting in Mexico. As part of a monitoring program of this species, in this chapter, we model the relationship of deer occupancy with habitat variables at different scales, in a location at the Tehuacán-Cuicatlán Biosphere Reserve, Mexico. We deployed 30 camera traps during each season (dry and rainy) from 2018 to 2020, for a total of 10,800 camera-trap days. We used single-season occupancy models to evaluate the covariates that affect the detection and occupancy of white-tailed deer at different landscape scales (50, 150, and 300 ha). The results indicate that the camera-trap model and sampling effort affect the detection probability, while the occupancy probability increases with the tropical dry forest dominated by *Mimosa* spp. trees and decrease the slope. Specifically, the richness of scrubs additionally explained the occupancy probability during 2018. A significant result is that in all cases, the effect of these covariates was driven at a landscape scale of 150 ha. This landscape scale is within the home range size reported for this deer species in tropical habitats, which could explain these results. In conclusion, the white-tailed deer has a wide local distribution in the study site, possibly as a response to its ample capacity for environmental tolerance, the extension of almost 5700 ha with good habitat quality,

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and the constant protection that local people carry out as part of the management plan for the species in the study area.

Keywords Conservation · Extensive UMA · Local distribution · Management · Monitoring · *Odocoileus virginianus* · Tropical dry habitat.

14.1 Introduction

The analysis of habitat use, resource selection, and space use has a long tradition in wildlife ecological studies and management (Morrison et al. 2012; Fletcher and Fortin 2018; Millspaugh et al. 2020). In particular, animal–habitat relationships tend to manifest at specific spatial scales (Boyce 2006; Gaillard et al. 2010). Thus, accurately identifying these scales is crucial for linking habitat selection patterns to the ecological processes giving rise to them (Heit et al. 2023). For example, landscape heterogeneity can influence the distribution of large herbivores (Kie et al. 2002), but the number of resources or cover type may affect habitat selection at home ranges scale (Webb et al. 2007; Dechen Quinn et al. 2013; Millspaugh et al. 2020). The scale at which populations use landscapes could be used to develop management plans, recommend harvest rates, and interpret harvest data of this deer species (Webb et al. 2007).

The study of the factors that affect or are associated with local distribution, population density, and habitat use/preference by the white-tailed deer *Odocoileus virginianus* has been conducted by using different conceptual and methodological approaches, and different temporal and spatial scales (Stewart et al. 2011). Among the approximations used at the population level, data have been obtained from indirect methods (tracks and pellet counts), and direct methods such as sightings along line transects, capture–recapture, and camera trapping (Forsyth et al. 2022), while at the individual level, radiotelemetry has been mainly used (DeYoung and Miller 2011). The data from field surveys have been analyzed through various approaches and statistical models such as simple linear regressions, generalized linear models, multivariate models, and others. Frequently, those analyses are conducted under the implicit assumption that the detection of all individuals was perfect; however, when this probability is less than 1.0, then these approaches may underestimate the analyzed parameters (Denes et al. 2015).

In the last decade, the use of hierarchical models (HMs) applied to the estimation of different parameters, such as occupancy, local abundance, population density, demographic rates, and others, has increased significantly (McCaslin et al. 2021). This approach models the ecological process (occupancy, density, or others) conditional on the probability of detection that is assumed to be imperfect (Royle and Dorazio 2008; Royle et al. 2013; Kéry and Royle 2016, 2020). In the case of ungulate species, there are examples of the application of HMs for different purposes (v.gr., Haus et al. 2019; Duquette et al. 2020; Messmer et al. 2020; Kumar et al. 2021; Baribeau et al. 2022). Thus, HMs represent an alternative approach to estimating local distribution using occupancy models, specially obtained with camera traps (O'Connell and Bailey 2011; Emmet et al. 2021; Murray et al. 2021). In the case of studies where the principal focus is resources selection, habitat use, and local distribution using presence–absence data (detection–no detection), and where the animals are not individually identified, the use of logistic regression and/or occupancy modeling (two linked logistic regressions, one for the ecological process conditional to the detection process) is a common technique (McClintock and Thomas 2019; Millspaugh et al. 2020; Thornton and Peers 2020).

The white-tailed deer is one of the most studied and exploited species throughout its geographical distribution range, covering a wide area in the Americas (Heffelfinger 2011). In Mexico, this species is found throughout the territory except in some northwestern regions (Ortega et al. 2011) and is a highly prized species to supplement the consumption of animal protein, trade, craftsmanship, recreation, and has been part of the cosmogony and rites of various indigenous cultures (Mandujano et al. 2014). In addition, the white-tailed deer is one of the main species managed in the northeastern region (Villarreal 1999), and with wide opportunities for management in the tropical zones of central and southeastern Mexico (Villarreal-Espino 2006; Mandujano 2016). This deer is the most important species in the wildlife management and conservation units (UMA for their Spanish initials) (Mandujano and González-Zamora 2009; Mandujano 2010), and the most frequently studied deer species in protected areas across the country (Gallina et al. 2007).

In the Tehuacán-Cuicatlán Biosphere Reserve (TCBR) are present wild ungulates such as the white-tailed deer (Fig. 14.1), collared peccary (*Pecari tajacu*), and red brocket deer (*Mazama temama*), and domestic ungulates such as goats (*Capra hircus*), cattle (*Bos taurus*), horses, and donkeys (*Equus* spp.) (Ortíz-García et al. 2012; Mandujano et al. 2019). The white-tailed deer represents an important resource for human communities within TCBR (Mandujano et al. 2016a). Subsistence hunting of white-tailed deer is a practice that has been carried out in the region for a long time, and recently, trophy hunting is present as well (López-Téllez et al. 2016). This species has been studied to understand its ecology and behavior and as part of a long-term monitoring project (Yañez-Arenas et al. 2012; Ramos-Robles et al. 2013; Barrera-Salazar et al. 2015; Yañez-Arenas and Mandujano 2015; Mandujano et al. 2016b). However, one aspect that has not been addressed in detail is the evaluation of the potential effects of some habitat and human factors at different spatial scales on the local distribution of this species.

The main objective of this study was to analyze habitat use by the white-tailed deer using camera-trap data from 2018 to 2020 in a selected location within TCBR. We quantified the relationships between landscape variables (vegetation types, topography, human factors, and vegetation structure variables) at different spatial scales (50, 150, and 300 ha) to explain habitat use by this deer. This allowed us to test whether the spatial scale and heterogeneity played a major role in determining the local distribution of the white-tailed deer, for which we employed hierarchical models to estimate its detection and occupancy probabilities. This information is essential to understand the ecology of this species in semiarid tropical habitats and to manage its populations for their conservation and sustainable use.

Fig. 14.1 White-tailed deer is an important ecological species in the Tehuacán-Cuicatlán Biosphere Reserve, Mexico

14.2 Methods

14.2.1 Study Area

The study was conducted in San Gabriel Casa Blanca in the state of Oaxaca, Mexico (17° 39′ - 18° 53′ N, 96° 55′ - 97° 44′ W; Fig. 14.2a). The site is located within the region La Cañada on its border with the Oaxacan Mixteca region. The site of approximately 5700 ha forms part of the Tehuacán-Cuicatlán Biosphere Reserve, which covers an area of 490,187 ha in the southeast of the state of Puebla and northeast of Oaxaca (Dávila et al. 2002). The site features a semiarid climate with an average temperature of 24 °C. Rainfall occurs in summer, and average annual precipitation is 438 mm. Land use is composed of 8% agriculture, 1% urban, 63% tropical dry forest, and 28% crassicaule scrub (Fig. 14.2c). The tropical dry forest is

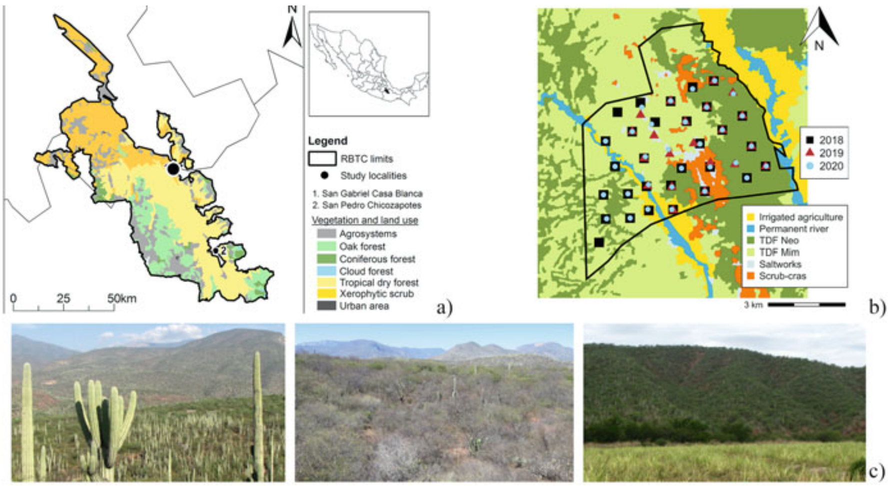

Fig. 14.2 (**a**) Geographical location of the Tehuacán-Cuicatlán Biosphere Reserve and study site at San Gabriel Casa Blanca, Oaxaca, Mexico; (**b**) camera-trap designs from 2018 to 2020; and (**c**) illustration of the tropical dry forest dominated by *Neobuxbaumia tetetzo* (Neo), tropical dry forest dominated by *Mimosa* spp. (Mim), and agricultural zone along rivers, respectively

characterized by the dominance of woody plants 8–10 m in high, with the dominant trees losing their foliage during the dry season. The crassicaule scrub plant community is characterized by large numbers of thick-stemmed succulents (Barrera-Salazar et al. 2015).

14.2.2 Camera-Trap Sampling

Sampling was conducted from January 2018 through November 2022 during the dry (December to May) and rainy (June to November) seasons, using 30 camera-trap stations with a single camera (Moultrie A30, Primos Truth Cam35, and Moultrie D55IR) each season/year. The cameras were deployed in a standardized randomized design where the first camera is randomly placed and the rest at an equidistant distance of about 1 km (Fig. 14.2b). In the field, the cameras were placed in woody vegetation or columnar cacti at approximately 30 cm above the ground. No baits or attractants were used. The cameras were checked every three months, and the images obtained were organized through the open-access photo manager software DigiKam, where each photo was identified and labeled with the species' scientific name through the EXIF metadata (López-Tello and Mandujano 2017). Subsequently, we used the *camtrapR* package (Niedballa et al. 2016) to organize and process the white-tailed deer records to construct the detection matrices. Because we were interested in knowing the effect of the year and the climatic season (rainy or dry) on deer occupancy, we constructed detection histories for each season and year, for a total of six detection matrices. In each story, we considered the site as each phototrapping station, and each occasion consisted of 7 consecutive days. Additionally, detection histories were adjusted to a maximum of 60 sampling days to minimize the risk of violating the closed population assumption (MacKenzie et al. 2017). We used the stacked detection matrices to model white-tailed deer occupancy, resulting in a matrix with 157 sites and 12 survey occasions.

14.2.3 Landscape and Habitat Covariates

We first defined the covariates at three spatial scales (50, 150, and 300 ha) considering the potential home range of this deer species, which could be less than 200 ha in tropical habitats (Gallina et al. 2010; Ortega et al. 2011; Mandujano et al. 2014). We named the landscape each of the buffers created around each camera trap to obtain areas of 50, 150, and 300 ha. Consequently, different landscapes were obtained depending on the buffer radii and the number of cameras each year (Fig. 14.3). For each buffer, we estimated the landscape composition and cover of each of the six vegetation types based on Barrera-Salazar et al. (2015). The vegetation types considered were: a tropical dry forest dominated by *Neobuxbaumia tetetzo* (Neo), tropical dry forest dominated by *Mimosa* spp. (Mim), crassicaule scrub (Cras), salt works (Salt), irrigated agriculture (Agri), and the course of the river (River). For each landscape, we measured the distance to the near human settlement, distance to a near-permanent river, distance to agricultural zones, slope, and aspect. Particularly, in October 2018 we obtained the species richness, cover, and density of trees and scrubs, sampling 30 sites around the camera traps (for details, see Zavatela et al. 2023). We used the R packages *raster* (Hijmans 2022), *GISTools* (Brunsdon and Chen 2014), and *landscapemetrics* (Hesselbarth et al. 2019), for the analysis of spatial data and to calculate landscape composition. An important aspect is that the overlapping landscapes (in this study at 300 ha) have already been shown not to affect the estimation because they are not pseudo-replicates (Zuckerberg et al. 2012). On the contrary, what affects the estimation is the spatial independence in terms of the distance between cameras (Zuckerberg et al. 2020).

14.2.4 Data Analysis

We used the single-species single-season occupancy models to evaluate the covariate effects on deer occupancy. We did not use a multiseason model because several sites did not function from season to season or year to year, which reduced the sample to fit a dynamic model requiring more data to generate robust estimates ($>$120 sites; Mckann et al. 2013). Additionally, we were not interested in modeling the rate of occupancy change (known as extinction or site colonization parameters).

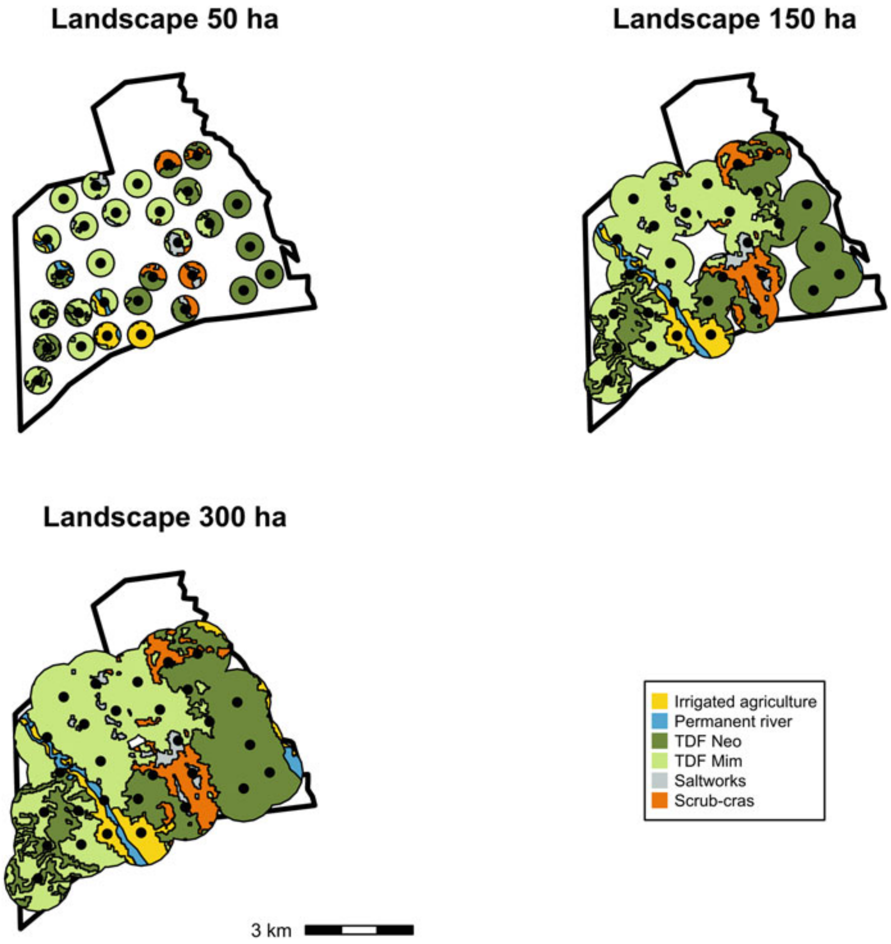

Fig. 14.3 Example of landscapes at three scales (50, 150, and 300 ha) around each camera trap during 2018

Therefore, we used the stacked modeling strategy that allowed us to model landscape covariables along with the effect of the years and climatic seasons for the one-season model.

We used a secondary candidate model selection strategy to select among different candidate models structure that represented covariate effects on occupancy and detection probability (Bromaghin et al. 2013; Morin et al. 2020). We used the Akaike Information Criterion (AIC) to independently rank candidate models for occupancy and detectability. The best ranking models for each process were combined in a final selection stage. In this last stage, we also explored the additive and multiplicative interactions of selected landscape variables with seasons or years. We selected the best models for each stage using an AIC <2 (Anderson 2008). To evaluate the selected models' goodness of fit, we used the MacKenzie and Beiley test (MacKenzie and Bailey 2004) with the *AICcmodavg* package (Mazerolle 2020). In the case of presenting one or more selected models, we based our inference on the one that presented the best fit under the MB test. Finally, for the 2018 data, the occupancy models analyzed were those that included variables of the tree and shrub stratum. The complete procedure for adjusting single and multispecies occupancy models was conducted with a maximum likelihood approach using the *unmarked* package (Fiske and Chandler 2011) in R 4.0.1 (R Core Team 2019). We applied the final better-fitted model to a raster map with an extent of 12,000 ha and a resolution based on the best-fitted model's result (150 ha), to predict the spatial occupancy probability for white-tailed deer in the entire study site.

14.3 Results

Considering the grouping of independent data every 7 days, a total of 360 detections ($n = 116$ in 2018, 116 in 2019, and 128 in 2020) were obtained (196 in the rainy season and 164 in the dry season) during a total of 10,800 camera-trap days sampling (Fig. 14.4).

The naive occupancy estimated from camera trapping varied between 63% and 80%, and it was higher during the rainy season. The white-tailed deer had a wide distribution in the study area during the dry and rainy seasons, and it was relatively stable throughout the years (Fig. 14.5). The number of detections was higher in the tropical dry forests dominated by giant cactus *Neobuxbaumia tetetzo* and by *Mimosa* spp. trees during the rainy and dry seasons of the three years sampled. However, there were variations in the use of the crassicaule scrub, agricultural areas, and salt zones (Fig. 14.6).

Fig. 14.4 Total detections and naive occupancy of white-tailed deer during the dry and rainy seasons from 2018 to 2020

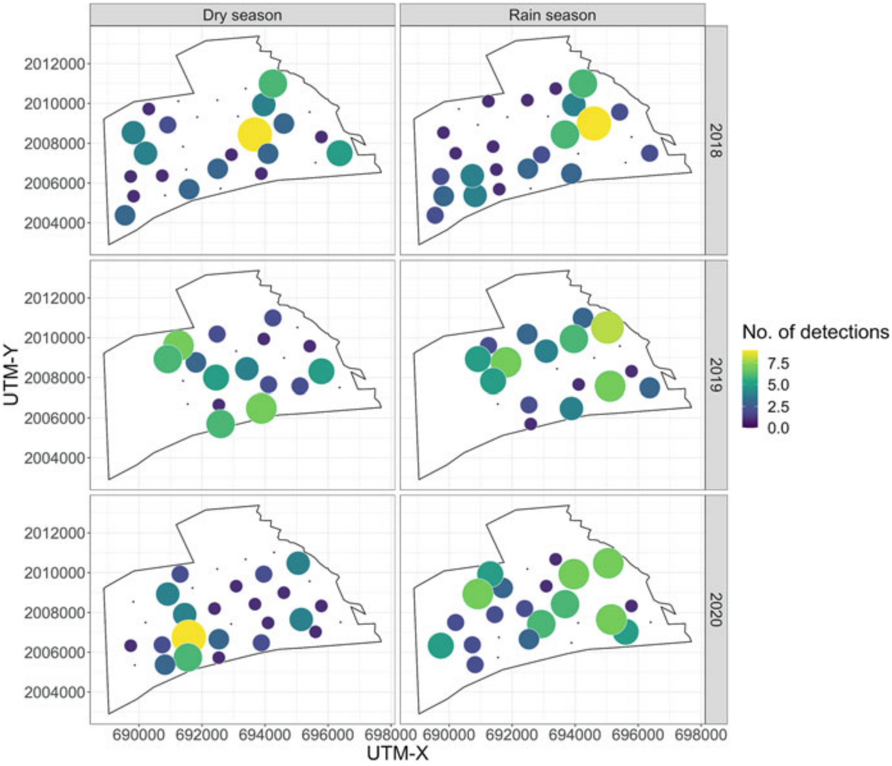

Fig. 14.5 Annual and seasonal distribution of white-tailed records per camera trap during the dry and rainy seasons from 2018 to 2020

Through our modeling strategy, we found that the probability of deer detection was influenced by the interaction between the camera-trap model and the sampling effort (Table 14.1). Regarding occupancy probability, the best model showed that deer selected the vegetation type dominated by *Mimosa* at a landscape scale of 150 ha (Table 14.1). The occupancy probability was 0.68 (SD = 0.07) and increased with *Mimosa* cover. This relationship was observed for both the rainy and the dry seasons (Fig 14.7a). Regarding the effect of the year and season, we found that the occupancy probability was greater during the rainy season. In addition, the probability of deer occupancy was higher in areas with gentler slopes (Table 14.1). The occupancy probability was 0.69 (0.07) and increased as the slope decreased (Fig 14.7a). The beta coefficients of these models are shown in Table 14.2.

For our 2018 modeling data, we found that occupancy was again best explained by the *Mimosa* at a landscape scale of 150 ha in relationship with the richness of scrubs and the diversity of tree species (Table 14.1). The occupancy probability was 0.97 (0.05) and increased with the richness of scrubs while decreased with the

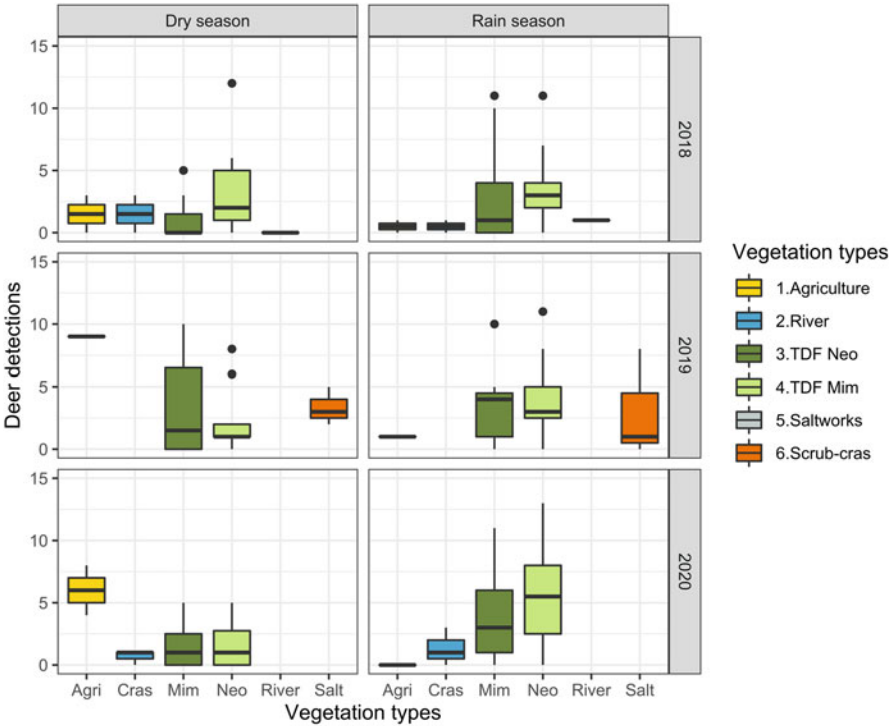

Fig. 14.6 Detections of the white-tailed deer at each vegetation type during the dry and rainy seasons from 2018 to 2020. The colors are according to the covers in Fig. 14.2b

diversity of trees (Fig 14.7b). The beta coefficients of these models are shown in Table 14.2.

Based on the better-fitted model that included tropical dry forest dominated by *Mimosa* spp. and distance to the near human settlement at a landscape scale of 150 ha (resolution) in the 12,150 ha (extent), we estimated the occupancy probability of the white-tailed deer in the study area (Fig 14.8a). Considering a $\psi > 0.85$, the highest occupancy probability was estimated for the central and western parts of the study location dominated by *Mimosa* in gentle slopes (<5°) and away from the largest human settlement. But considering a ψ between 0.70 and 0.85, white-tailed deer were also found in the vegetation type dominated by the giant cactus *Neobuxbaumia tetetzo* in the western mountainous region of the study area (slopes >15°).

Table 14.1 Logistic models to test the detection probability (p) and occupancy probability (ψ) of the white-tailed deer in the study area. We include here only p and ψ mean (± SD) of the better fitted models (Delta AIC < 2)

Models	K	AIC	Delta_AIC	Model_Lik	AIC _Wt	ψ	p	c_ hat	P
Effect of detection									
p(Cam* effort) ψ(.)	7	1410.68	0.00	1.00	0.94	0.79 (0.04)	0.16 (0.05)	1.18	0.12
p(Cam* Season) ψ(.)	7	1417.85	7.16	0.03	0.03	–	–	–	–
p(Cam* Year) ψ(.)	10	1418.10	7.42	0.02	0.02	–	–	–	–
p(Cam) ψ(.)	4	1420.55	9.87	0.01	0.01	–	–	–	–
p(effort) ψ(.)	3	1437.35	26.67	0.00	0.00	–	–	–	–
p(Seasson) ψ(.)	3	1447.23	36.55	0.00	0.00	–	–	–	–
p(Year) ψ(.)	4	1447.91	37.23	0.00	0.00	–	–	–	–
p(.) ψ(.)	2	1451.22	40.53	0.00	0.00	–	–	–	–
Effect of landscape scale (50, 150, and 300 ha) on vegetation types									
p(Cam*Effort) ψ(Mim_150)	8	1405.75	0.00	1.00	0.61	0.68 (0.07)	0.14 (0.04)	1.28	0.12
p(Cam*Effort) ψ(Mim_300)	8	1408.20	2.45	0.29	0.18	–	–	–	–
p(Cam*Effort) ψ(Mim_50)	8	1411.05	5.30	0.07	0.04	–	–	–	–
p(Cam*Effort) ψ(Neo_150)	8	1411.31	5.56	0.06	0.04	–	–	–	–
p(Cam*Effort) ψ(Neo_300)	8	1411.40	5.65	0.06	0.04	–	–	–	–
p(Cam*Effort) ψ(Cras_50)	8	1411.99	6.24	0.04	0.03	–	–	–	–
p(Cam*Effort) ψ(Cras_150)	8	1412.44	6.69	0.04	0.02	–	–	–	–
p(Cam*Effort) ψ(Cras_300)	8	1412.55	6.80	0.03	0.02	–	–	–	–
p(Cam*Effort) ψ(Neo_50)	8	1412.68	6.93	0.03	0.02	–	–	–	–
p(Cam*Effort) ψ(.)	7	1417.85	12.10	0.00	0.00	–	–	–	–
p(.) ψ(.)	2	1451.22	45.47	0.00	0.00	–	–	–	–
p(.) ψ(Cras_150)	3	1452.68	46.93	0.00	0.00	–	–	–	–
p(.) ψ(Cras_300)	3	1452.69	46.94	0.00	0.00	–	–	–	–
p(.) ψ(Mim_300)	3	1452.94	47.19	0.00	0.00	–	–	–	–

(continued)

Table 14.1 (continued)

Models	*K*	AIC	Delta_AIC	Model_Lik	AIC _Wt	ψ	*p*	c_ hat	*P*
p(.) ψ(Cras_50)	3	1452.94	47.19	0.00	0.00	–	–	–	–
p(.) ψ(Mim_50)	3	1452.99	47.24	0.00	0.00	–	–	–	–
p(.) ψ(Mim_150)	3	1452.99	47.24	0.00	0.00	–	–	–	–
p(.) ψ(Neo_150)	3	1453.08	47.33	0.00	0.00	–	–	–	–
Effect of season and year									
p(Cam* effort) ψ(Mim_150+ Season)	9	1405.98	0.23	0.89	0.35	0.62 (0.09)	0.14 (0.04)	1.29	0.10
p(Cam* effort) ψ(Mim_150*Season)	10	1407.77	2.02	0.36	0.14	–	–	–	–
p(Cam* effort) ψ(Mim_150+ Year)	10	1409.27	3.52	0.17	0.07	–	–	–	–
p(Cam* effort) ψ(Mim_150 * Year)	12	1410.73	4.98	0.08	0.03	–	–	–	–
p(.) ψ(.)	2	1451.22	45.47	0.00	0.00	–	–	–	–
Effect of human activity and slope									
p(Cam* effort) ψ(Mim_150 + slope)	9	1407.60	0.00	1.00	0.80	0.69 (0.07)	0.14 (0.04)	1.27	0.12
p(Cam*effort) ψ(Mim_150 + dist_Agri)	9	1411.65	4.05	0.13	0.11	–	–	–	–
p(Cam* effort) ψ(slope)	8	1411.87	4.27	0.12	0.09	–	–	–	–
p(Cam* effort) ψ(dist_Agri)	8	1417.59	9.99	0.01	0.01	–	–	–	–
p(.) ψ(.)	2	1451.22	43.61	0.00	0.00	–	–	–	–
p(Cam* effort) ψ(dist_pob)	8	1467.24	59.64	0.00	0.00	–	–	–	–
p(Cam*effort) ψ(Mim_150+ dist_pob)	9	1536.72	129.11	0.00	0.00	–	–	–	–
p(Cam*effort) ψ(Mim_150+ dist_pob + slope)	10	1538.72	131.11	0.00	0.00	–	–	–	–
Effect of vegetation structure during 2018									
p(Cam) ψ(Mim_150 + R_arb)	6	419.77	0.00	1.00	0.40	0.97 (0.05)	0.01 (0.01)	1.34	0.09
p(Cam) ψ(Mim_150 + Div_Arb)	6	421.39	1.62	0.45	0.18	0.96 (0.04)	0.01 (0.01)	1.45	0.07
p(Cam) ψ(Mim_150 + Div_arb)	6	424.40	4.63	0.10	0.04	–	–	–	–
p(Cam) ψ(R_arb)	5	482.26	62.49	0.00	0.00	–	–	–	–
p(Cam) ψ(Div_Arb)	5	492.39	72.62	0.00	0.00	–	–	–	–

p(Cam) ψ(Div_arb)	5	493.50	73.72	0.00	0.00	–	–	–	–
p(.) ψ(.)	2	506.57	86.80	0.00	0.00	–	–	–	–

Abbreviations: Parameters (K), model likelihood (ModLik), weight AIC (AICWt), cumulative weight (Cum.Wt), (c-hat), (P), camera-trap model (Cam), trap-days (Effort), 2018–2020 (Year), dry or rainy seasons (Season), tropical dry forest dominated by *Neobuxbaumia tetetzo* (Neo), tropical dry forest dominated by *Mimosa* spp. (Mim), crassicaule scrub (Cras), distance to the near human settlement (Dist_Pob), distance to agricultural zone (Dist_Agri), richness of scrubs species (R_Scrubs), diversity of trees (Div_Arb) and scrubs (Div_arb)

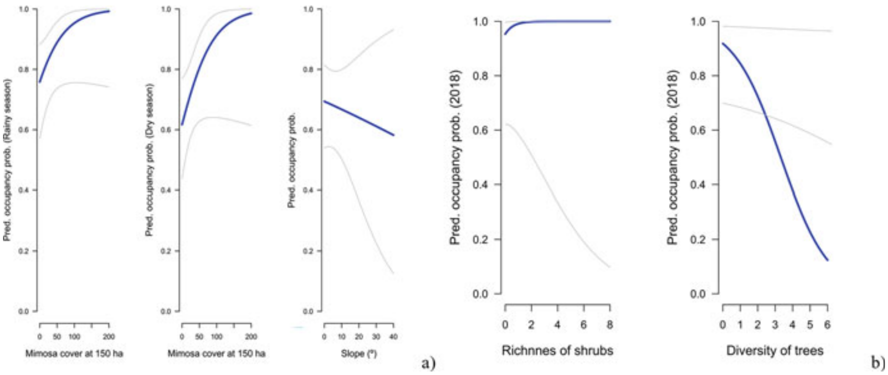

Fig. 14.7 Probability of occupancy (ψ) of landscape at scale of 150 ha by white-tailed deer in relation to (**a**) tropical dry forest dominated by Mimosa trees during the dry and rainy seasons, and slope from 2018 to 2020; and (**b**) richness of scrubs and diversity of trees during 2018

Table 14.2 Estimation of beta (β) coefficients for the top-ranked models of occupancy probability (ψ) of the white-tailed deer

Model/variables	*B*	SE	*z*	*P*
~Cam * Effort ~ Mim_150				
Intercept	0.76	0.31	2.48	0.01
Mim_150	0.02	0.01	1.83	0.07
~Cam * Effort ~ Mim_150 + Season				
Intercept	0.48	0.37	1.29	0.20
Mim_150	0.02	0.01	1.80	0.07
Season_Rainy	0.67	0.51	1.30	0.19
~Cam * Effort ~ Mim_150 + Slope				
Intercept	0.82	0.34	2.42	0.02
Mim_150	0.02	0.01	1.82	0.07
Slope	−0.01	0.03	−0.39	0.70
~Cam ~ Mim_150 + R_arbus				
Intercept	3.44	1.50	2.30	0.02
Mim_150	1.25	1.04	1.20	0.23
R_arbus	1.79	1.12	1.60	0.11
~Cam ~ Mim_150 + Div_Arb				
Intercept	3.22	1.13	2.86	0.00
Mim_150	2.76	1.12	2.47	0.01
Div_Arb	−0.78	0.50	−1.57	0.12

14.4 Discussion

Our results suggest that the local distribution of white-tailed deer is wide and consistent between the dry and rainy seasons from 2018 to 2020 in the study area. Based on the naive occupancy and number of detections (nonhierarchical modeling), this deer species was used more frequently in the tropical dry forest dominated by the giant cactus *Neobuxbaumia tetetzo* and by *Mimosa* trees and scrubs species, which

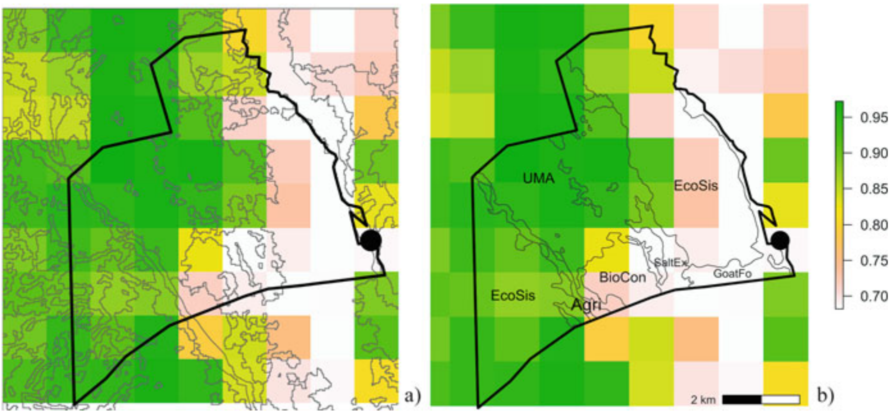

Fig. 14.8 (**a**) Prediction of spatial occupancy probability by white-tailed deer in relation to the cover of tropical dry forest dominated by *Mimosa* trees, and to slope, at a landscape scale of 150 ha (square grids) in the 12,150 ha of extent area. Gray lines represent the polygons of vegetation types (see Fig. 14.2). (**b**) Spatial occupancy probability in relation to the land use planning map (gray lines) for the sustainable use and conservation of natural resources in the study site. Abbreviations: EcoSis Ecosystem Services, UMA Wildlife Management Unit, BioCon Biological Conservation zone, Agri Agriculture, SaltEx Salt Exploitation, GoatFo Goat Foraging zone. (Based on CONAFOR 2012). The black point represents the San Gabriel Casa Blanca locality

are widespread in the study area. Previous estimates of the population density of this deer based on fecal group counts (Ramos-Robles et al. 2013; Barrera-Salazar et al. 2015) confirmed this trend in the use of extant habitat. This use could be related to the availability and selection of plants by this cervid in the study site (Vasquez et al. 2016), and to the general habitat quality conditions using habitat suitability models (Fabian-Rosas 2015; Montero-Montiel 2016). Therefore, these results show the great adaptability of the white-tailed deer to the conditions of dry tropical habitats (Mandujano 2010), and possibly also to the protection provided by residents.

Our results through the application of hierarchical occupancy modeling suggest that habitat occupancy probabilities of the white-tailed deer are best explained by the vegetation type dominated by *Mimosa* trees, the slope, and the richness of scrub species primarily during the rainy season at a landscape scale of 150 ha. Considering that the occupancy is the result of animal activities, the first possible biological explanation for these results is the home range of this deer species. It is known that individuals of any species must satisfy their habitat requirements mainly by selecting resources (food, water, cover, and others) that maximize their survival and reproduction (Horne et al. 2020). In the case of the white-tailed deer, there is a lot of information about its home range size and its explaining factors (sex, age, vegetation types, resources availability, seasons, and others), particularly in the northern regions of its geographic range (v.gr., Webb 2005; DeYoung and Miller 2011; Stewart et al. 2011). In contrast, few studies have estimated home range sizes smaller than 200 ha (Gallina et al. 2010; Ortega et al. 2011; Mandujano et al. 2014; Gallina-

Tessaro et al. 2019) and even smaller than 100 ha (Rojas et al. 1997; Contreras-Moreno et al. 2021) in tropical regions. Daily traveled distances by the white-tailed deer are in relation to seasonality and reproductive phenology in tropical habitats (Contreras-Moreno et al. 2019). Here we are not suggesting that the home range is 150 ha in the study site, but it is significant that this scale best explains the occupancy by white-tailed deer, and that scale falls within the potential range of activity of the species in tropical habitats. Other studies measured landscape metrics within varying radii (250, 500, 1000, and 2000 m) from each deer's home range center and found that 57% of the variation in the home range size of mule deer (*O. hemionus*) was explained at a scale of 2000 m radii in a northern geographical location (Kie et al. 2002). These authors highlighted the potential importance of spatial scale and heterogeneity in determining the distribution and habitat use of large herbivores. This strongly suggests the importance of modeling the effect of spatial scale on habitat use for this and other species (v.gr., Presley et al. 2019; Alves et al. 2020).

Our results suggest that occupancy probabilities are best explained by *Mimosa* trees found on gentle slopes of less than 10° in the central and western parts of the study area. For our sampling of 2018, our results suggest that the occupancy probability is better explained by the number of scrub species during the rainy season again in the sites dominated by *Mimosa* at landscapes of 150 ha. This area is characterized by a lower tree stratum and higher scrubs presence, in a relatively open habitat, and near vegetation dominated by *Neobuxbaumia tetezo* in hilly sites. This creates ecotones o transition zone formed by different vegetation (see Fig. 14.2). This deer species is well adapted to relatively open scrub habitats in heterogeneous landscapes and exploit ecotone sites (Stewart et al. 2011). The occupancy probability of the *Mimosa* zone was higher during the rainy season when food availability and cover to protection is higher. In addition, during the rainy season, the fawns are born, and it is common to find photos on camera traps of adult females accompanied by young. During the dry season, young and adult males are observed more frequently, although this aspect has not yet been studied in detail at this site. We do not know if there is seasonal sex segregation at this site, as has been documented in other studies (DeYoung and Miller 2011). Finally, another factor that was not included in the modeling is the spatiotemporal movements of goat herds. The goats forage principally in the eastern zone and near the human establishment (Pérez-Solano et al. 2020) where the habitat use by the white-tailed is lower (Fig. 14.8b). In contrast, goat herds use the study site's central and western zones less frequently.

14.5 Conservation and Management Implications

Our results could have an important application for the sustainable use and conservation of the white-tailed deer in our study area. The scale at which populations use landscapes could be used to develop management plans (Webb et al. 2007). In the San Gabriel Casa Blanca community, a land management plan guides the use and

Fig. 14.9 Hunting of white-tailed deer males for local consumption and as game trophies is an important activity in the Wildlife Management Unit (UMA) at San Gabriel Casa Blanca, Oaxaca, Mexico

conservation of natural resources elaborated by the local people (CONAFOR 2012). Our analyses clearly showed that the zone where the UMA and the area underpayment for environmental services are located in the central and western sectors coincide with the area with the highest occupancy probability by the white-tailed deer (Fig 14.8b). The spatial prediction of occupancy probability by the white-tailed deer agrees with what local people know about the species and resources into their land, as has been shown in other studies (v.gr., Brittain et al. 2022). Therefore, the protection actions carried out by local people for several years have probably benefited wildlife populations and their habitats in this location and could represent an excellent example of conservation in the Tehuacán-Cuicatlán Biosphere Reserve (Fig. 14.9).

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Chapter 15
Overview of Hierarchical Models and Future Directions in the Study of Neotropical Mammals

Gabriel P. Andrade-Ponce

Abstract This chapter provides a concise overview of the hierarchical models that are commonly used in the literature and throughout this book. Its purpose is to offer the reader a comprehensive understanding of models underlying structure and rationale. The chapter describes the basic occupancy model, along with its extensions for multiseason and multispecies analyses. Furthermore, it elucidates the N-Mixed and Royle–Nichols models, which are employed for abundance estimation. In addition to these, the chapter expounds upon the hierarchical approximation of the distance model, utilized for species density estimation, and explores spatially explicit capture–recapture models for estimating both abundance and density of species through individual recognition.

Keywords Distance · hierarchical models · N-mixture · occupancy · spatial capture–recapture

15.1 Description of the Most Common Hierarchical Models

As mentioned in the previous sections, hierarchical models are born as a conceptual and analytical tool that allows us to separate the observational and the ecological process, so that it is possible to distinguish the effect of each process on our inference or prediction. We can formally define hierarchical models as sequences of linear models (general or generalized) connected or conditioned to each other by the probability structure they represent (Kéry and Royle 2015). The "simplest" models present only two processes, one model describing the ecological state variable and another describing the logistic process (e.g., occupancy models; MacKenzie et al. 2002). However, the levels of a hierarchical model can increase depending on the objectives, geographical scale, or level of inference (Guillera-Arroita 2017; Koshkina et al. 2017; Devarajan et al. 2020; Fernández-López et al. 2023). For a

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deeper understanding of the models, in this chapter, we will briefly describe some of the most common ones.

15.2 Basic Detection/No Detection Models and Its Extensions

15.2.1 Occupancy Models

Occupancy models are hierarchical models that have two levels: one level or model that describes the ecological process, which in this case is the presence or absence of the species; and another level that describes the observational process, which is the ability to detect or not detect the species, given that it is present (MacKenzie et al. 2017a). To estimate these two parameters, the occupancy models are based on matrices or histories of detection and nondetection of species (ones and zeros) at certain sites. In other words, we need to visit each site several times (occasions or surveys) (MacKenzie et al. 2017a). Before describing the model, it is important to mention that the definition of the site (minimum spatial unit) and sampling occasion (minimum temporal unit) could affect the estimation and interpretation of the model, therefore be defined following the research question, and reported in any investigation (Efford and Dawson 2012; Bailey et al. 2014; Steenweg et al. 2018).

For the occupancy models, the state variable that describes the presence or absence in each site (i) is defined by the letter z ($z = 1$, presence; $z = 0$, absence). This state variable follows a Bernoulli distribution with probability ψ (psi). In other words, ψ is the probability of occupancy, use, or presence (MacKenzie et al. 2017a). The algebra notation for the ecological process is:

$$z_i \sim \text{Bernoulli}(\psi_i)$$

For the observational process, the y_{ij} is the measurement of detection in each site i in each survey occasion j. As for z, y follows a Bernoulli distribution with detection probability p. The result of the observational process is conditional to z because is the product of z and p. This product is since to if a species is not present at a site, then it will not be possible to detect it. Then we have this algebraic notation:

$$y_{ij} \mid z_i \sim \text{Bernoulli}(z_i p)$$

As can be seen, these two processes are two generalized linear models of the Bernoulli error family and as such, the occupancy and detection probabilities can be modeled by different covariates. This can be done simply with a link function such as logit, like this:

$$\text{logit}(\psi_i) = \beta_0 + \beta_1 x_i$$

where β_0 represents the intercept and β_1 the slope coefficient for the covariate x taken at each site i. The same logic applies to the detection process (p), except that in this case, we can include variables taken for each site i or each occasion j.

As in any statistical model, hierarchical models must meet assumptions to generate unbiased estimates. In occupancy models, these are: (1) that the occupancy status of each site does not change during the sampling period. This assumption is known as the closed-site assumption. In this case, it is therefore important to define a sampling period and site area so that an occupied site does not become unoccupied due to the species demographics process (MacKenzie et al. 2017b). This assumption can be relaxed in some cases where the species enters and leaves the site randomly, in which case the occupancy is interpreted as "use" of the site (Efford and Dawson 2012; Steenweg et al. 2018). (2) The probability of detection and occupancy should be the same for the different occasions or sites respectively. Otherwise, they should be modeled by using covariates. (3) Detections should be independent for each event (temporal independence) and sampling site (spatial independence). (4) There must be certainty in the identification of the species, i.e., there can be no false positives.

15.2.2 Occupancy Multiseason

In some cases, the climatic season, disturbances, or species population processes generate changes in species occupancy or abundance for each site. Therefore, the interest is to monitor how the occupancy status changes as a function of time. To address this type of question, it is necessary to use a dynamic approach, which explicitly considers the rate of change of the parameter of interest in each sampling season. Naturally, a single-season occupancy model, as well as the other models described in this chapter, can be extended to accomplish this task (Kéry and Royle 2020). In the literature, you will find them as dynamic or multiseason occupancy models (MacKenzie et al. 2017c).

Multiseason models require sampling data from several sites (i) with repeated visits (j), with the difference that these samples must now be repeated in several seasons (t) for the same sites (Kéry and Royle 2020). This allows the definition of two additional parameters: the probability of colonization (γ) and local extinction (ϵ). The first one γ_t defines the probability that a site not occupied in season t will be occupied in the following season (t + 1). While ϵ_t is defined as the probability that an occupied site in season t, will be unoccupied in the following season (t + 1) (MacKenzie et al. 2003). By including the new parameters, the algebraic notation is similar to the one-season occupancy model but includes the transition processes that also follow a Bernoulli distribution, thus:

$$
\begin{aligned}
z_{1,i} &\sim \text{Bernoulli}(\psi_i)\\
(z_{t,i}|z_{t-1,i}=0) &\sim \text{Bernoulli}(\gamma_{t-1}) \text{ for } t=2,\ \ldots, T,\\
(z_{t,i}|z_{t-1,i}=1) &\sim \text{Bernoulli}(1-\epsilon_{t-1}) \text{ for } t=2,\ \ldots, T,\\
y_{t,ij} \mid z_{t,i} &\sim \text{Bernoulli}(z_{t,i}p_t)
\end{aligned}
$$

In this case, $z_{1,\ i}$ denotes the latent occupancy estate for season 1, so that for $t = 2$, $z_{t,\ i}$ depends on the state of the previous season. Thus, when the species is present in unit i in the previous season ($z_{t,\ i}|z_{t\ -\ 1,\ i} = 1$), it will be present in season t with probability $1 - \epsilon_{t\ -\ 1}$ (the probability that it is not "extinct" in that unit). Whereas when the species was absent for the previous season ($z_{t,\ i}|z_{t\ -\ 1,\ i} = 0$), the species will be present in season t with a probability γ_t. Following the same logic as in the simple model, each parameter can be modeled as a function of covariates using a link function such as logit.

The dynamic model follows the same assumptions as the single occupancy model, only now the closed-site assumption applies for each season, but not between seasons. Hence, in time t, the occupancy status of each site must be maintained within t but may change in t + 1. In addition, we now also assume that if there is heterogeneity in the parameters of occupancy status change (γ y ϵ) this should be modeled with the inclusion of covariates (MacKenzie et al. 2017c).

15.2.3 Occupancy Models for Multispecies

Many questions in ecology involve more than one species and consequently, there are also hierarchical model approaches to address these questions. In the specific case of occupancy, models that consider two or more species are known as multispecies occupancy models. We can divide multispecies models into two groups: (1) those focused on species co-occurrence and (2) those focused on estimating species community metrics (Devarajan et al. 2020).

Hierarchical co-occurrence models aim to determine how the occupancy of one species affects another, correcting for the imperfect detectability of each (MacKenzie et al. 2017d). Several parameterizations can be used depending on the objectives of the study and we can divide the parameterizations into two groups: conditional and nonconditional. Conditional parameterization assumes a dominant (A) and a subordinate species (B) so that occupancy of the subordinate species is always calculated conditional to the dominant species. Thus, the model in its ecological process can define the occupancy parameters of the dominant species (ψ^{A}), the occupancy of the subordinate species when the dominant species is present ($\psi^{B|A}$), and the occupancy of the subordinate species when the dominant species is absent ($\psi^{B|a}$) (Waddle et al. 2010; Richmond et al. 2010). The subordinate and dominant species can be defined based on ecological criteria (e.g., larger competitor is dominant over the smaller one), but they can also be defined based on the researcher's interest. For example, we are interested in knowing how the occupancy of a predator changes as a function of its prey, so in this case, the predator will be the subordinate species in the model. Note that this parameterization only allows the inclusion of two species and assumes an asymmetrical relationship. Sometimes there is no a priori expectation of dominant or subordinate relation of species, so a no-conditional parameterization could be used (MacKenzie et al. 2004, 2021; Rota et al. 2016). For example, Rota et al. (2016) model uses a multivariate Bernoulli distribution with a random variable per possible pair species state: the presence of A in absence of B, the presence of B in the absence of A, the presence of both species, the absence of both species and so on, depending on species numbers (Rota et al. 2016). This not only allows modeling interactions between two or more species and assumes a symmetrical relationship between species. However, it is important to consider that including more species in the co-occurrence model implies the estimation of more parameters and thus requires a greater amount of data (Clipp et al. 2021; Kéry and Royle 2021). Finally, is necessary to know that although co-occurrence models are used to investigate ecological interactions, the co-occurrence patterns are the result of a variety of processes. So, caution must be taken to interpret the co-occurrence outputs of this kind of models (Holt 2020; Andrade-Ponce et al. 2022).

Multispecies community models were developed to estimate different aspects of the biological community, such as richness considering imperfect detection, and even other metrics of taxonomic and functional diversity (Broms et al. 2015; Jarzyna and Jetz 2016; Guillera-Arroita 2017). Depending on the research objective and the metric of interest, the model specification may change (Kéry and Royle 2015). However, here we will describe the "simple" three-level model, without including derived parameters such as species richness that require data augmentation techniques (Dorazio and Royle 2005).

In this model the occupancy of each species k at each site i is modeled following a Bernoulli distribution with probability ψ_{ki}

$$Z_{ki} \sim \text{Bernoulli}(\psi_{ki})$$

Here, Z_{ki} represents the occupancy status value for the species at each site. Similarly, the detection of each species k, at each site i and sampling occasion j, is modeled with a Bernoulli distribution with probability p. As in the previous models, the probability p will be conditional on the presence of the species, i.e., on Z

$$y_{kij} \mid Z_{ki} \sim \text{Bernoulli}\left(p_{kij} * Z_{ki}\right)$$

where y_{kij} represents the detection status of each species, at each site and for each sampling occasion. The third level model includes the effect of each species as random, which assumes that the species-specific effects come from a normal distribution for the logit of ψ and p, thus:

$$\text{logit}(\psi_k) \sim \text{Normal}\left(\mu_{l\psi}, \sigma^2_{l\psi}\right)$$

$$\text{logit}(p_k) \sim \text{Normal}\left(\mu_{lp}, \sigma^2_{lp}\right)$$

In this way, we can obtain an estimate at the community level but also at the species level assuming that the species occupancy parameter in the community comes from the same distribution (ψ_k or p_k). This is important for the design since the sampled species must present similar characteristics to be detected in the same way (given that they are present) by the sampling method (Guillera-Arroita et al. 2019). Because multispecies models estimate large numbers of parameters, they tend to be data-hungry and therefore require large numbers of sites and detections to generate robust estimates. Discussions on the limitations, considerations, and sampling design for applying this type of model can be found in Devarajan et al. (2020) and Guillera-Arroita et al. (2019).

15.3 Abundance N-Mixture Models

15.3.1 Detection Heterogeneity or Royle–Nichols Model

As in the basic occupancy models, Royle–Nichols (RN) models use repeated sampling to obtain detection–no detection data (Royle and Nichols 2003). However, RN model has the advantage of considering the possible heterogeneity in the probability of detection given by the natural abundance of the study species (Royle and Nichols 2003). This is particularly important when it is not possible to measure or identify the quantiles in the variation of detection in a study since such heterogeneity can generate biases in the estimation of occupancy (McClintock et al. 2010). These characteristics make the RN a special model, since it can be considered as an occupancy model with heterogeneity in detection (Murray and Sandercock 2020) or an N-Mixture model given the difference in probability distribution of its processes (just as we will see below) (Kéry and Royle 2015). Because the RN model connects the heterogeneity of the detection with the abundance distribution, it is also possible to obtain an abundance estimate with this type of model. To understand how this model works we can look at its algebraic notation:

$$y_{ij} \mid N_i \sim \text{Bernoulli}\left(P_{ij}\right)$$

$$P_{ij} = 1 - \left(1 - p_{ij}\right)^{Ni}$$

Just as in the occupancy models y_{ij} is the measure of detection for each site i on each occasion j, which in this case is conditional on N_i which is the abundance for each site i. The difference is that in this case the probability of detection is given by P_{ij} which depends on the probability of detection per individual p on each j occasion

N_i. This dependence p_{ij} and N_i implies that if the species is more abundant at the site, it will have a higher probability of being detected (Dorazio 2007). The relationship of both parameters also makes the model assume that the probability of detection of the species varies for each site, as does its abundance.

The ecological process is based on the probability distribution of abundance and can follow a Poisson distribution, as follows:

$$N_i \sim \text{Poisson}(\lambda_i)$$

As already mentioned, N_i is the latent variable for the number of animals at each site i and λ is the expected abundance for each site i. Again, both detection and abundance can be modeled along with covariates using the link function. Although it is not a direct part of the model formulation, the occupancy can be derived from it. This is achieved due to the relationship between abundance and occupancy, since when $N_i > 0$, then $z_i = 1$. Mathematically, the occupancy probability can be obtained as:

$$\Psi = 1 - \exp(-\lambda)$$

15.3.2 N-Mixture Models

As in the occupancy and Royle–Nichols models, N-mixed models are based on a series of samples for each defined site (Royle and Dorazio 2009). However, in N-mixed models, the base data correspond to counts of individuals, so the state variable is the population size N_i (Royle 2004). Since now our state or ecological variable is abundance, it is possible to model it by a Poisson distribution (negative binomial or zero-inflated distributions are also possible) as follows:

$$N_i \sim \text{Poisson}(\lambda_i)$$

where λ is the expected abundance for each site i. It is also possible to use negative binomial distribution when the probability of success is low, as well as zero-inflated distributions when a large number of unoccupied sites are sampled (Wenger and Freeman 2008). For the observation level, the counts y_{ij} assumed a Binomial distribution conditional of the true population size at each site i. As you can see the observational process is now binomial because we are not dealing with just the detection or not at each site (zeros and ones), but the number of detections for each site. Additionally, p is now the probability of detection for each individual. This differs from the occupancy models where p is the probability of detection of the site. The algebraic notation is as follows:

$$y_{ij} \mid N_i \sim \text{Binomial}(N_i, p)$$

Looking at both processes, it is clear what the name "N-mixture" refers to, since we have the conjunction of binomial/Poisson models (Kéry and Royle 2015). It is possible to use covariates to model both processes with the help of a link function, as in occupancy models, except that in count models the most common is in log link function.

15.4 Distance Sampling

15.4.1 Hierarchical Distance Model

Distance sampling has been widely used in wildlife ecology and consists of mature conceptual development (Buckland et al. 2015). In this type of sampling, transects or counting points are used where the distance at which each detected individual is taken. The recording distance allows measuring the probability of detection of individuals, so that the greater the distance, the lower the ability to detect, and at a minimum distance there is no imperfect detection. Formally, these models include a function of detection of an individual as a function of its distance, which allows having a "corrected" abundance estimate (Buckland et al. 2015). However, in these classical distance models, the inference is focused on the detection component, with N being a general estimate. As a result, the spatial variation of N for each transect is not considered (Hedley and Buckland 2004; Kéry and Royle 2015).

The subsequent development of what is known as the hierarchical distance model (HDM), allows density or abundance to be modeled as a latent variable and its spatial variation to be considered (Royle et al. 2004). In its simplest version, the HDM uses grouped units or categories of observation distances of individuals. Thus, there are h distance classes, with y number of counts per distance at each site i, which is conditional on the population size of N_i and follows a multinomial distribution:

$$y_{i1}, \ldots\ldots, y_{ih} \sim \text{Multinomial}(N_i, \pi_i)$$

where π is the multinomial probability for each distance h at each site i and depends on the distance encounter detection probability σ (Kéry and Royle 2015). As in the other models, the local abundance variable N_i, assumes a Poisson probability distribution with the expected abundance of λ for each site i.

$$N_i \sim \text{Poisson}(\lambda_i)$$

15.5 Capture–Recapture Models

15.5.1 Spatial Capture–Recapture Models

Up to this point we have been talking about models based on individuals that cannot be recognized, but there is a long-standing family of models based on the capture and recapture of recognizable or marked individuals (capture–recapture models or CR models; Efford 2004). Capture–recapture models use an individual encounter history over certain periods or occasions *j*. Very similar to what we saw with the data structure of the other models, as the hierarchical models of untagged species were based on the principles of capture–recapture models (MacKenzie et al. 2017a). The detail of the specific parameterization of each RC model is beyond the scope of this book and as mentioned there is extensive literature on this type of model (Pollock 2000; Amstrup et al. 2005; King and McCrea 2019). However, here we will describe one of the most robust approximations for the estimation of the density and abundance of tagged animals, the spatially explicit capture–recapture models (SCR) (Royle et al. 2014; Harmsen et al. 2020).

The SCRs are not limited to being a simple extension of the CR models, since they explicitly develop the spatial organization of the sample arrangement and the movement and use of space (Murray and Sandercock 2020). For this purpose, the models use the capture histories including the spatial component. In this way, each recognized individual's center of activity (s), also called the centroid of the home environment, is estimated. The totality of these activity centers constitutes the state space (S), which is the observation window in which the possible activity centers of the population are distributed. We can describe the simplest model as follows:

$$N \sim \text{Poisson}(\mu||S||)$$

where N is the number of activity centers and μ is the number of points per unit area S or population density. For the simplest model, we can assume that N activity centers are distributed uniformly in the polygon S:

$$s_i \sim \text{Uniform}(S)$$

In the SCRs, the observational process is defined by the distance function p for each device j and each individual i. This function describes the distance between the individual's center of activity and the location of the capture device, like distance models. In this model $p0$ is the probability of detecting an individual activity centre right at the location of the sampling device x_j, and σ is the seminormal distribution parameter that defines the rate at which the probability of detection decreases as the distance between the activity center and the sampling device increases.

$$p_{ij} = p_0 \exp\left(\frac{-\left\|x_j - s_i\right\|^2}{2\sigma^2}\right)$$

Thus, the observation process is defined by y_{ij} conditional on the center of activity of each individual i and follows a Bernoulli distribution with probability p_{ij}

$$y_{ij} \mid s_i \sim \text{Bernoulli}\left(p_{ij}\right)$$

The model components can be modified depending on the objectives, sampling design, and data structure. For example, to estimate population dynamics over time (i.e., open population models; Efford and Schofield 2020), models that allows for the inclusion of information on unmarked individuals (Chandler and Royle 2013; Jiménez et al. 2021), or integrate information for resource selection (Royle et al. 2013) and so on. An in-depth guide to these models can be found in Royle et al. (2014).

15.6 Future Directions

The Neotropics (sensu *lato* Morrone 2014) host an extraordinary diversity of mammalian species, including endemic groups such as opossums, xenarthrans, and caviomorph rodents (Patterson and Costa 2012; Burgin et al. 2018). Approximately 1600 mammal species, constituting 30% of world mammal diversity, are recognized for the neotropics, occupying different biomes including tropical forests, savannas, scrublands, and deserts (Burgin et al. 2018). However, this region has also endured significant anthropogenic transformations during the twenty-first century (Ceballos et al. 2017), resulting in approximately 18.8% of mammalian species being categorized as threatened (Vulnerable, Endangered, or Critically Endangered) (Túnez et al. 2021). The scarcity of ecological knowledge concerning these species, combined with the rapid degradation of natural habitats in the Neotropics, poses a substantial challenge in terms of designing effective conservation plans and mitigation strategies. Consequently, it becomes imperative to generate ecological information and gain a comprehensive understanding of the processes influencing the distribution, abundance, and richness of Neotropical mammals (Sutherland et al. 2004).

Over the past decade, hierarchical models (HMs) have emerged as crucial analytical tools for monitoring species distribution and abundance, primarily due to their ability to disentangle observational effects from ecological processes and their remarkable flexibility (Guillera-Arroita 2017; Kéry and Royle 2020). This book demonstrates the immense potential of HMs in generating valuable insights into the abundance of various Neotropical mammal species and unraveling the diverse ecological processes shaping their habitat use. Numerous examples in the literature highlight large-scale studies utilizing HM models, providing crucial information regarding species responses to habitat changes (Semper-Pascual et al. 2020, 2021) and estimates of abundance across species distributions (Schank et al. 2017). Conservation science and research in tropical regions hold substantial potential for leading the use and development of hierarchical models. The increasing availability and accessibility of data present opportunities to advance the field of HMs, enabling the study of population dynamics and temporal processes (Kéry and Royle 2020). Moreover, incorporating data integration from multiple sources to enhance estimations (Koshkina et al. 2017; Jiménez et al. 2022; Fernández-López et al. 2023) and explicitly incorporating spatial aspects into models and ecological inquiries (Olea and Mateo-Tomás 2011; Sutherland et al. 2014; Zhao et al. 2017) open up productive avenues for studying Neotropical mammals.

While HMs are a relatively new and expanding field in our region, we anticipate that a growing number of ecologists and conservation professionals will recognize and appreciate the advantages (as well as the limitations) offered by HMs. However, it is crucial to acknowledge that models serve as tools and are valuable when accompanied by robust ecological theories and appropriate sampling designs (González-Maya et al. 2018; Andrade-Ponce et al. 2021). Therefore, we encourage the development of approximations and hierarchical approaches tailored to the unique nature of data, conservation challenges, and research priorities specific to the Neotropics.

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