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

S. Mandujano (✉)
Red de Biología y Conservación de Vertebrados, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico
e-mail: salvador.mandujano@inecol.mx

E. J. Naranjo
Departamento de Conservación de la Biodiversidad, El Colegio de la Frontera Sur, San Cristóbal de Las Casas, Chiapas, Mexico

G. P. Andrade-Ponce
Posgrado, Instituto de Ecología A. C., Xalapa, Veracruz, Mexico

S. Mandujano et al. (eds.), *Neotropical Mammals*,
https://doi.org/10.1007/978-3-031-39566-6_1

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

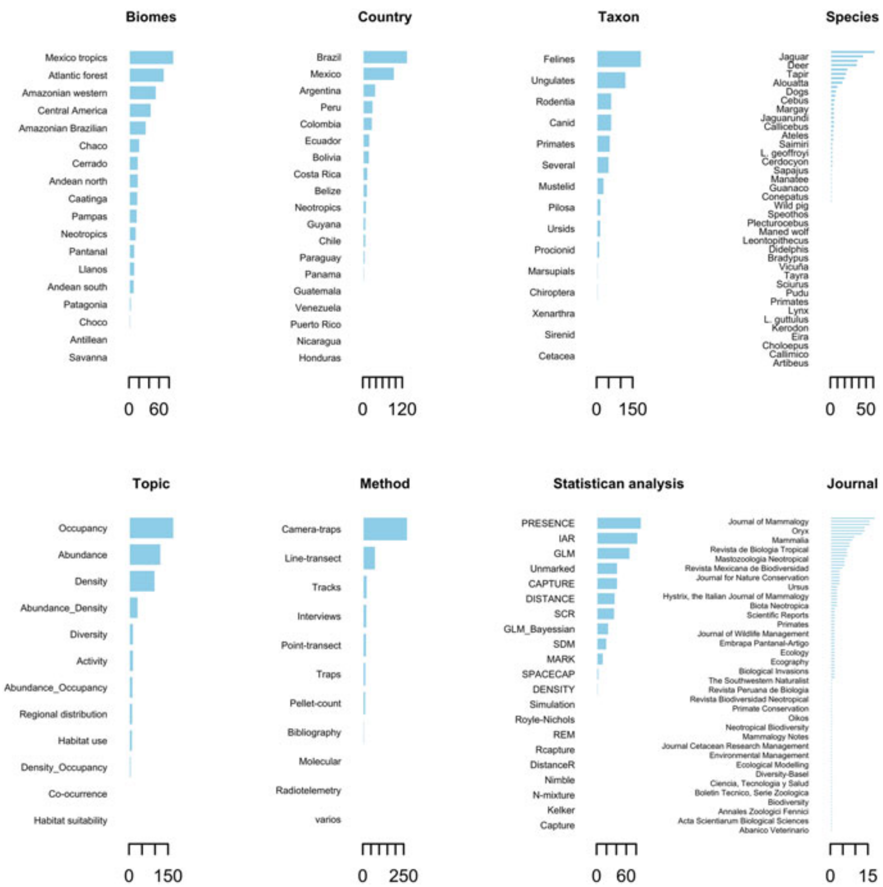

Fig. 1.1 Frequency of the papers ($n = 309$) referring to the study of Neotropical mammals according to the different classifications (biomes, country, bowl, species, topics studied, methods, statistical analyses, and journals in which the works were published)

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

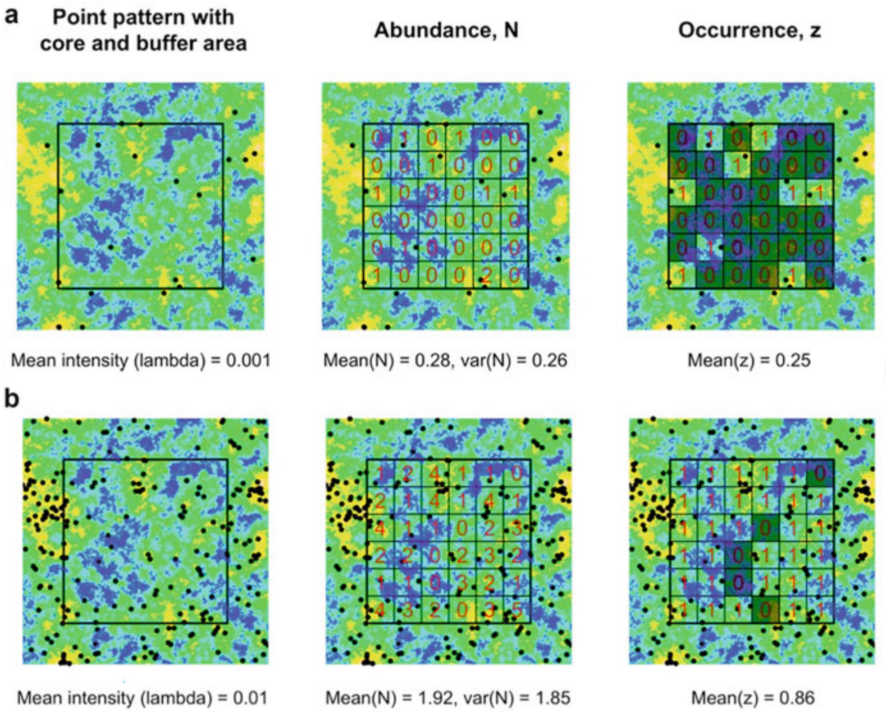

Fig. 1.2 Two examples of the relationships between the point pattern, abundance, and occurrence. The intensity of the lambda parameter is lower in (**a**) than in (**b**). The simulations were produced by the *simPPe* function of the AHM package. (Kéry et al. 2022)

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.

References

Andrewartha HG, Birch LG (1954) The distribution and abundance of animals. University of Chicago Press, Chicago

Buckland ST, Rexstad EA, Marques TA, Oedekoven CS (2015) Distance sampling: methods and applications. Springer International Publishing, Cham

Burgin CJ, Colella JP, Kahn PL, Upham NS (2018) How many species of mammals are there? J Mammal 99(1):1–14

Carrillo JD, Forasiepi A, Jaramillo C, Sánchez-Villagra MR (2015) Neotropical mammal diversity and the Great American Biotic Interchange: spatial and temporal variation in South America's fossil record. Front Genet 5:451. https://doi.org/10.3389/fgene.2014.00451

Ceballos G, Ehrlich PR, Raven PH (2020) Vertebrates on the brink as indicators of biological annihilation and the sixth mass extinction. Proc Natl Acad Sci 117(24):13596–13602

Costa LP, Leite YL, Mendes S, Ditchfield AD (2005) Mammal conservation in Brazil. Conserv Biol 19(3):672–679

Denes FV, Silveira LF, Beissinger SR (2015) Estimating abundance of unmarked animal populations: accounting for imperfect detection and other sources of zero inflation. Methods Ecol Evol 6(5):543–556

Dirzo R, Ceballos G, Ehrlich PR (2022) Circling the drain: the extinction crisis and the future of humanity. Philos Trans R Soc B 377:20210378. https://doi.org/10.1098/rstb.2021.0378

Eisenberg JF (1989) Mammals of the Neotropics, vol. I: the northern Neotropics. University of Chicago Press, Chicago

García del Valle Y, Naranjo EJ, Caballero J, Martorell C, Ruan-Soto F, Enríquez PL (2015) Cultural significance of wild mammals in Mayan and mestizo communities of the Lacandon Rainforest, Chiapas, Mexico. J Ethnobiol Ethnomed 11:36. https://doi.org/10.1186/s13002-015-0021-7

Kéry M, Royle A (2016) Applied hierarchical modeling in ecology: analysis of distribution, abundance, and species richness in R and BUGS, vol 1. Elsevier Academic Press, Waltham

Kéry M, Royle A (2020) Applied hierarchical modeling in ecology: analysis of distribution, abundance, and species richness in R and BUGS, vol 2. Elsevier Academic Press, Waltham

Kéry M, Schaub M (2012) Bayesian population analysis using WinBUGS: a hierarchical perspective. Elsevier Academic Press, Waltham

Kéry M, Royle A, Meredith M (2022) AHMbook: functions and data for the book ‘applied hierarchical modeling in ecology’, vols 1 and 2. R package version 0.2.6. https://CRAN.R-project.org/package=AHMbook

Krebs CJ (1978) Ecology: the experimental analysis of distribution and abundance. University of British Columbia, Vancouver

MacKenzie DI, Nichols JD, Royle JA, Pollock KH, Bailey LL, Hines JE (eds) (2017) Occupancy estimation and modeling, 2nd edn. Academic, Boston

Magurran AE, McGill BJ (2010) Biological diversity: frontiers in measurement and assessment. OUP, Oxford

Nagy-Reis M, Oshima JE, Kanda C, Palmeira FB, De Melo F et al (2020) Neotropical carnivores: a data set on carnivore distribution in the Neotropics. Ecology 101(11):e03128. https://doi.org/10.1002/ecy.3128

Ojeda RA (2013) Diversity and conservation of Neotropical mammals. In: Levin SA (ed) Encyclopedia of biodiversity, vol 2, 2nd edn. Academic, Waltham, pp 582–594

Patterson BD (2020) On drivers of Neotropical mammal diversification. Mastozool Neotrop 27:15–26

Patton JL, Pardiñas UFJ, D’Elia G (2015) Mammals of South America, vol. 2 (Rodents). The University of Chicago Press

Royle JA, Dorazio RM (2008) Hierarchical modeling and inference in ecology: the analysis of data from populations, metapopulations and communities. Elsevier, Waltham

Royle JA, Chandler RB, Sollmann R, Gardner B (eds) (2014) Spatial capture-recapture. Academic, Boston

Simpson GG (1980) Splendid isolation: the curious history of South American mammals. University Press, New Haven

Solari S, Martinez-Arias V (2014) Recent changes in systematics and taxonomy of Neotropical bats (Mammalia: Chiroptera). Therya 5:167–196. https://doi.org/10.12933/therya-14-180

Thompson WL (2004) Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters. Island Press, Washington, DC

Valdez R (2019) Historical and conservation perspectives of wildlife in Mexico. In: Valdez R, Ortega JA (eds) Wildlife ecology and management in Mexico. Texas A&M University Press, College Station, pp 1–18