Chapter 6
Survey Methods and Hierarchical Modeling for Mexican Primates

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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.

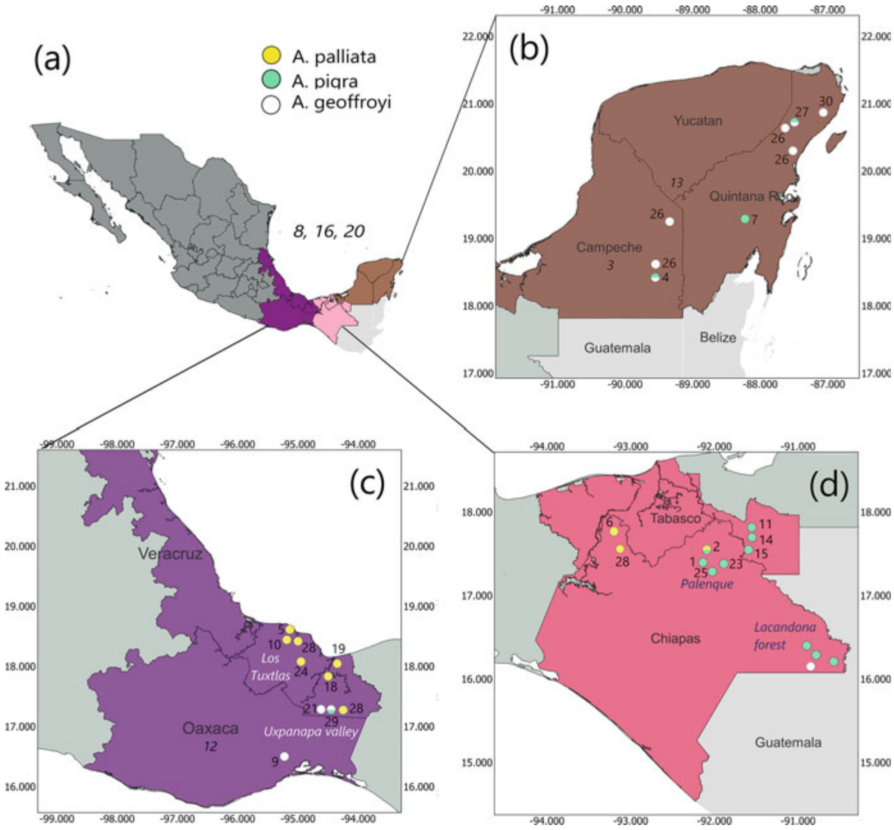

Fig. 6.2 Map of primate surveys carried out in Mexico since 2002. Highlighted areas in (**a**) show the Mexican multistate regions where surveys took place, and (**b**–**d**) show the specific locations where survey studies were carried out in each area. Numbers coincide with study IDs from Table 6.2. 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

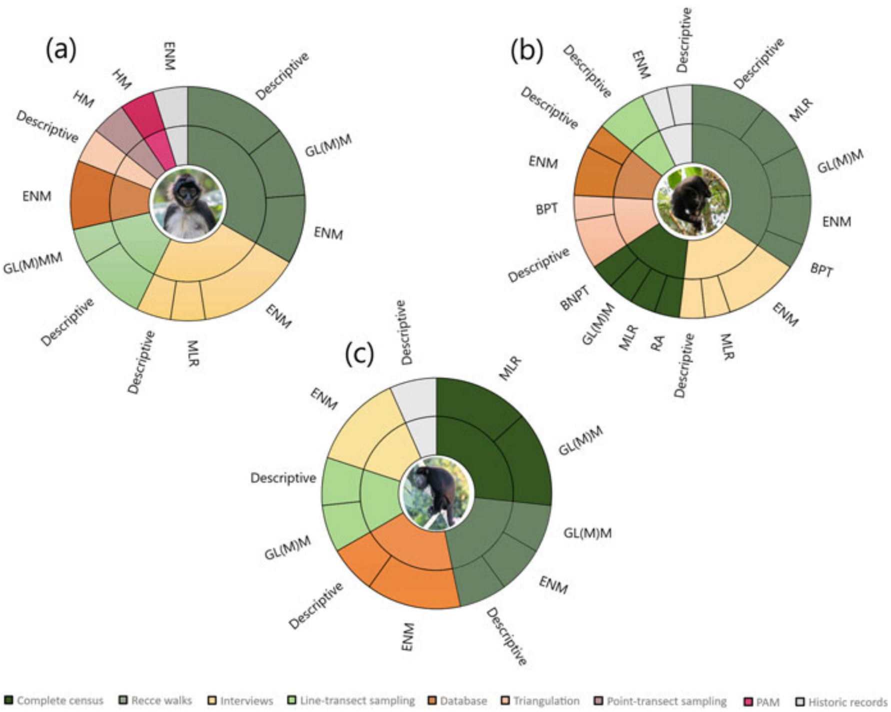

Fig. 6.3 Survey methods (the inner circle) and corresponding data-analysis methods (outer circle) were reported for studies on (**a**) *Ateles geoffroyi,* (**b**) *Alouatta pigra*, and (**c**) *Alouatta palliata*. Descriptive Descriptive statistics or not reported, HM Hierarchical modeling, GL(M)M Generalized 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.

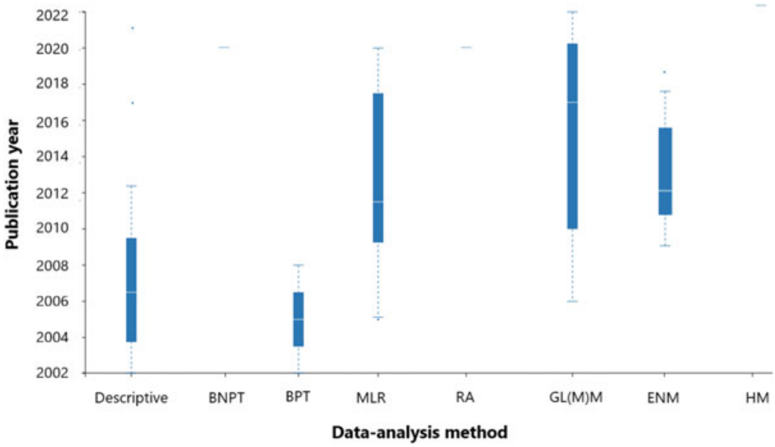

Fig. 6.4 Data-analysis methods used in the 30 reviewed studies plotted by their year of publication. When multiple data-analysis methods were used in the same study, we report the statistical approach with the highest complexity among them (see Table 6.3 for the degree of complexity). Boxplots show minimum 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.

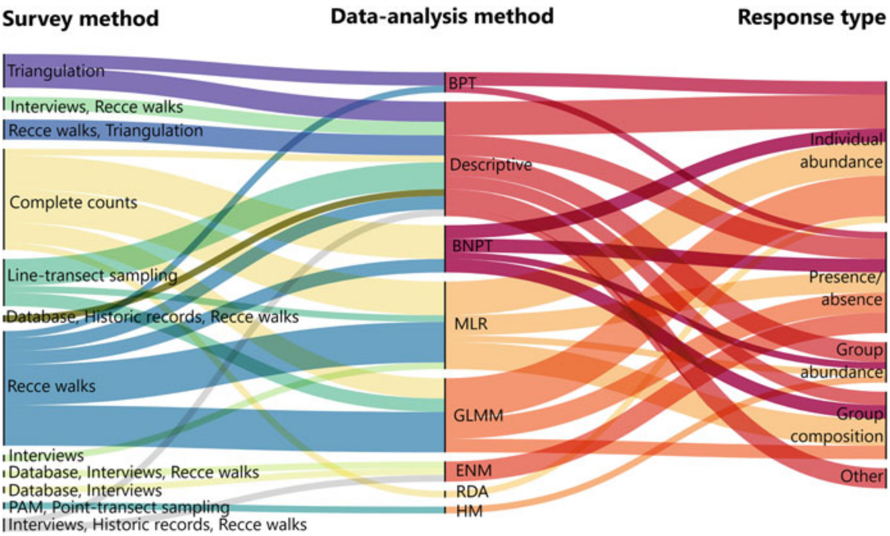

Fig. 6.5 Combinations of survey methods, data-analysis methods, and types of response variables used in the 30 studies (based on 57 data points as multiple types of data-analysis methods and response variables were used in 18 studies). Colored lines connect survey methods with the data-analysis methods 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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