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Occupancy and Detection Probabilities for Three Anuran Species that Differ in Habits and Risk Category in a Conserved Tropical Forest in Mexico

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***Abstract.*—Quantitative data about animal populations are essential for developing monitoring and conservation strategies. Occupancy estimation is a useful tool for monitoring species that are difficult to detect (e.g., many amphibian species) and to assess how environmental variables affect species distributions. We evaluated how the environmental characteristics of a conserved tropical forest in southern Mexico affect the occupancy and detectability of three anuran species: Chamula Mountain Brook Frog (*Duellmanohyla chamulae*), Berkenbusch's Robber Frog (*Craugastor berkenbuschii*), and Vaillant's Frog (*Lithobates vaillanti*). We initially estimated two parameters, occupancy and detection probabilities of these anuran species, and subsequently we evaluated how several environmental variables affect both parameters. We sampled the three species in 40 plots at two sites in Santa María Chimalapa, Oaxaca, southern Mexico, and we fitted species-specific single-season occupancy models. *Craugastor berkenbuschii* had the highest estimated occupancy (0.82), followed by *L. vaillanti* (0.66) and *D. chamulae* (0.25). We observed positive relationships of *D. chamulae* occupancy and detectability with elevation and temperature, respectively. Additionally, we found a positive relationship between *C. berkenbuschii* detectability and relative humidity, and we observed negative relationships between the occupancy of both *C. berkenbuschii* and *L. vaillanti* and the number of trees in the plots. Our study provides insight into how these three anuran species respond to habitat conditions and provides a baseline for future long-term research focused on species that inhabit preserved tropical forests.**

Key Words.—amphibian; conservation; *Craugastor berkenbuschii*; detection; *Duellmanohyla chamulae*; *Lithobates vaillanti*; tropical wet forest

Introduction

Monitoring vulnerable animal populations is critical for biodiversity conservation (Van Dyke 2008). Among terrestrial vertebrates, amphibians are the most threatened group because of worldwide population declines and many species extinctions (Luedtke et al. 2023). Almost 41% of assessed amphibian species are categorized as Threatened on the International Union for Conservation of Nature (IUCN) Red List (IUCN 2024). Because of their vulnerable status, it is important to assess the population status of amphibians through quantification of their abundance and distribution patterns (Oropeza-Sánchez et al. 2021).

Capture-mark-recapture methods, along with long-term monitoring surveys, enable the estimation of population size and other population parameters (i.e., growth, mortality, and survival rates; Mellor et al. 2004). Nonetheless, capture-mark-recapture methodologies in amphibians present challenges, including ethical concerns, efficacy, and the longevity of marking techniques. Some marking methods may affect the survival and fitness of amphibians (May 2004), and others involve handling individuals, which could increase their stress levels and negatively influence their survival (Fonner et al. 2017). Moreover, capture-mark-recapture methods

may be invasive (which can cause a certain degree of physical damage and alter the inherent behavior of an individual), difficult to apply, and short term (Ferner 2007), which may lead to over- or underestimation of population parameters (Otis et al. 1978; Lindberg 2012). Such effects potentially may bias research outcomes and thereby compromise the research objectives and conservation efforts (Guillera-Arroita 2017).

Occupancy models explicitly account for the imperfect detectability of animals under natural conditions by implementing probability methods that require only detection/nondetection data for each species (MacKenzie et al. 2002). Not only are these models an alternative to capture-mark-recapture methods, but occupancy estimation methods (MacKenzie et al. 2002) also allow us to quantitatively assess species that are difficult to capture, handle, and mark. These models can also quantify the influence of environmental variables on the probability that a species will occur at a particular site (Mackenzie et al. 2018; Oropeza-Sánchez et al. 2021). As a result, occupancy models can help determine species distributions within a landscape or region and provide insights into the preferred habitats and biotic conditions (Bendik et al. 2016). Additionally, occupancy modeling is useful for evaluating how land-use change affects species distributions (Roloff et al. 2011; Eskew et al. 2012).

We analyzed the occupancy probability of three species with different natural histories and threatened statuses that occupy different environments. The first species was the Berkenbusch's Robber Frog (*Craugastor berkenbuschii*), which is classified by the IUCN (2024) as Least Concern (LC) and by the Mexican authorities as a species Subject to Special Protection (Pr; Secretaría de Medio Ambiente y Recursos Naturales [SEMARNAT] 2010). This species prefers highly preserved habitats and inhabits areas near rocky streams (IUCN, Species Survival Commission, Amphibian Specialist Group [IUCN ASG] 2020a). The second species, the Vaillant's Frog (*Lithobates vaillanti*), also classified as Least Concern (LC; IUCN 2024) and is absent from the Mexican list of endangered and protected species (SEMARNAT 2010). It is frequently encountered in anthropogenically disturbed habitats, often associated with both permanent and temporary water bodies, including ponds, as well as streams (IUCN ASG 2020b). Finally, the Chamula Mountain Brook Frog (*Duellmanohyla chamulae*), listed as Endangered (EN; IUCN 2024) and as a species Subject to Special Protection (Pr) by the Mexican authorities (SEMARNAT 2010), inhabits preserved humid forests and cascading mountain streams (IUCN ASG 2020c).

Our aims were twofold: to calculate occupancy and detectability probabilities of the aforementioned anuran species based on single-season occupancy models (MacKenzie et al. 2002); and to assess the influence of different environmental conditions on the occupancy and detectability of these species. Our study, which was conducted in a preserved tropical forest, provides insight into the ecological associations of these species within a natural environment with minimal anthropogenic disturbance. Our results could serve as a baseline or reference for other studies that evaluate the spatial patterns of amphibians in natural and preserved areas or as a comparison with respect to the site occupancy of amphibians in disturbed environments.

Materials and Methods

Study area.—We conducted this study in the Los Chimalapas region of the southeastern part of the state of Oaxaca, southern Mexico (Fig. 1). This area, also referred to as Selva Zoque, shares its eastern border with the La Sepultura region in the state of Chiapas, Mexico (16°00'32" to 17°32'00"N, 93°21'40" to 94°53'53"W). The Los Chimalapas region is part of a large mountain chain called Sierra Madre de Chiapas, and is characterized by a diverse landscape comprising mountains, hills, glens, and valleys (De Teresa 2000; Ortiz-Pérez et al. 2004). The elevation in the region ranges from 90 to 2,300 m (De Teresa 2000). The original vegetation consisted mainly of Tropical Wet Forests, Cloud Forests, Tropical Dry Forests, and Pine-Oak Forests (Miranda and Hernández-X 1963; De Teresa 2000; Torres-Colín 2004). Currently, the landscape consists of secondary forests, agricultural and livestock fields, and large areas of preserved forests (Arriaga et al. 2000). The climate is mostly tropical wet-dry with a mean annual temperature that ranges from 22° to 26° C and a mean annual precipitation between 1,500 and 2,000 mm (Trejo 2004).

We conducted our study in two sites within the Santa María Chimalapa municipality: Monte Plata (16°49'2.73"N, 94°39'51.07"W) and Cerro Azul (16°52'57.89"N, 94°43'24.57"W; Fig. 1). Both sites are characterized by preserved tropical wet forests with hills and glens that have permanent streams. The elevation in these sites ranges from 250 to 550 m.

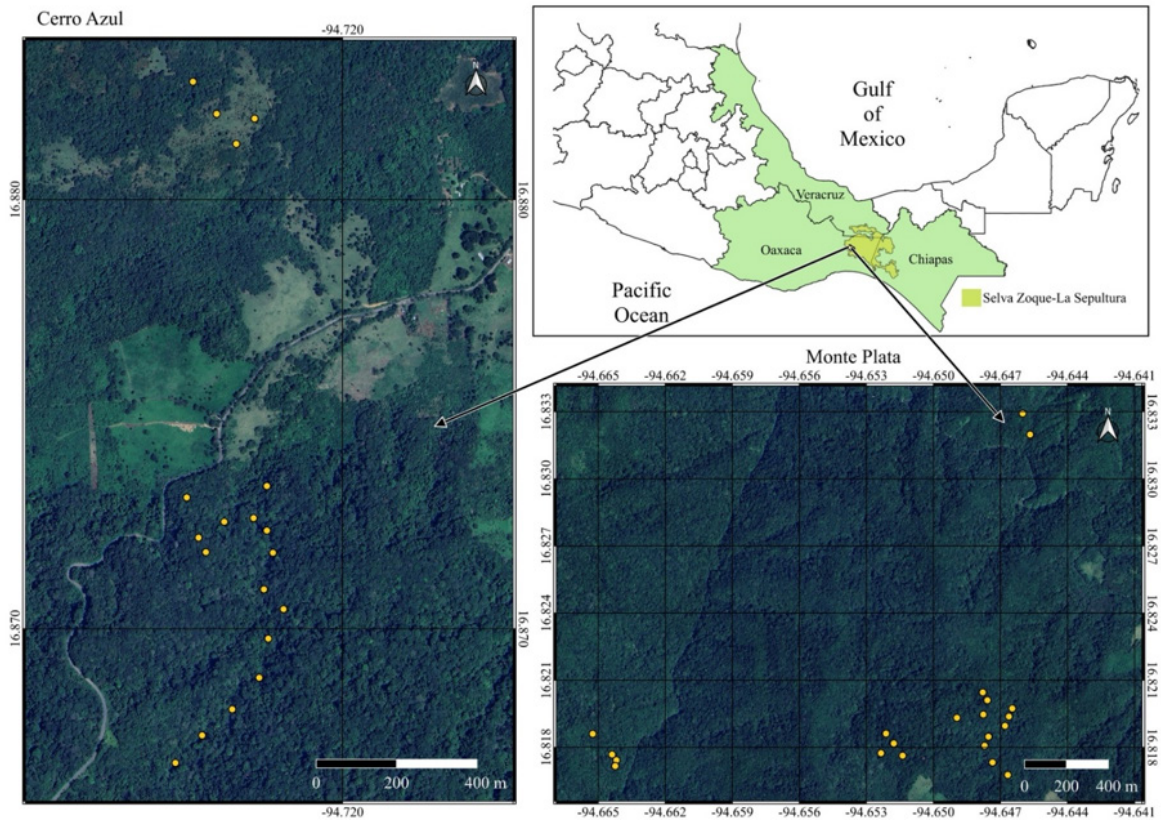

FIGURE 1. Location of the polygon Selva Zoque -La Sepultura (Los Chimalapas region) in the three Mexican states of Oaxaca, Veracruz, and Chiapas, and the locations of the two sites in Oaxaca that we sampled (Cerro Azul and Monte Plata). Yellow circles represent the sampled plots. (Images are from Google Earth; Google, Mountain View, California, USA).

Study design and data collection.—In December 2019, we conducted an initial visit to assess amphibian diversity and community structure in the two sites. We sampled amphibians for nine nights using Visual Encounter Surveys, which consisted of actively searching for amphibians in their preferred microhabitats (i.e., logs, litter, and under rocks; Crump and Scott 1994). We systematically searched for individuals of amphibian species across various topographic features, such as streams, riparian slopes, foothills, and mountaintops.

Based on the data collected, we plotted a rank-abundance curve following the method outlined by Magurran (2004). The relative abundance represents the logarithmic scale of the relative abundance of each species (PAi) plotted against their species rank (Sri), with species arranged from the most to the least abundant (Appendix Figure). Subsequently, we identified species that had different habits (arboreal, terrestrial, and semiaquatic) and were among the most frequently recorded in the anuran community, aiming to evaluate their occupancy probabilities.

At each site, we established 20 plots measuring 20 × 20 m, covering a total area of 400 m², with a minimum separation of 100 m between each plot (the maximum distance was 1,311 m, the minimum was 100 m, and the mean distance between plots was 186 m) to ensure independence in plot-specific detection probabilities. We collected data during the cold-humid season, in October 2021, with surveys that we conducted on three separate occasions, using a Visual Encounter Survey method (Crump and Scott 1994). We conducted surveys on consecutive days to meet population closure assumptions (Mackenzie et al. 2002). Specifically, two people surveyed 40 plots over 3 d, with each survey session lasting 15 min. Given the predominantly nocturnal behavior of study species, we conducted surveys between 2000 and 0200 (Crump and Scott 1994). We did not handle any individuals during this study; they were only visually detected and then recorded.

We recorded environmental variables at each plot, as these variables may influence the activity patterns of amphibians and consequently impact the detection of individuals (Walls et al. 2011). We

measured temperature and relative humidity using a thermohydrometer positioned at the midpoint of each plot. We recorded the elevation of each plot and its distance to the nearest water body. In addition, we quantified the number of herbaceous plants with a minimum height of 5 cm and the number of small trees (1–3 cm diameter at breast height [DBH]), medium trees (3.1–30 cm DBH), and large trees (> 30 cm DBH; Hernández-Ordoñez et al. 2019).

Target species.—During the initial site visit, we documented 12 amphibian species (two salamanders and 10 anurans). A rank-abundance curve indicated that the hylid frogs *D. chamulae* and the Cloud Forest Stream Frog (*Ptychohyla euthysanota)* were the most abundant species, followed by *C. berkenbuschii*, the Matuda's Spikethumb Frog (*Plectrohyla matudai*), and *L. vaillantii* (Appendix Figure). With the purpose of examining different drivers of site occupancy, we selected *D. chamulae*, *C. berkenbuschii,* and *L. vaillanti* as target species because they differed in habitat use (arboreal, terrestrial, and semiaquatic, respectively), average body size, skin color, and geographic distribution. Other candidate species (*P. euthysanota* and *P. matudai*) share a similar natural history with *D. chamulae* and belong to the same family.

Data analysis.—Based on plot-specific detection histories, occupancy models yield two main parameters: occupancy (ψ) and detection (*p*) probabilities. The first represents the probability of certain species being present in the area, whereas the second indicates the probability of detecting at least one individual of the species given that it is present (MacKenzie et al. 2002; Bailey and Nichols 2009). We built plot-specific detection histories for each species, in which we used 0 to denote that the target species was not detected during a particular sampling occasion and 1 to denote that the species was detected. We applied single-season occupancy models to our detection histories to estimate occupancy (ψ) and detection (*p*) probabilities by means of maximum-likelihood routines (MacKenzie et al. 2002). We estimated both parameters by fitting competing linear models separately for each species using program MARK (White and Burnham 1999; Gerber et al. 2009).

First, we fitted a null model where the environmental variables did not affect either of the parameters (i.e., both occupancy and detection probabilities remained constant across all plots). Then, we implemented models with all the combinations of predictors of ψ and *p*, using a single predictor variable per parameter in each competing model (Lebreton et al. 1992; Muths et al. 2006). We used both temperature and relative humidity as the predictor variables for the detection probability of the three species. We used elevation, distance to the nearest water body, number of herbaceous plants, and number of trees in each of our three categories based on their size (small, medium, and large trees) as the predictor variables for the occupancy probability of the three species. All the combinations of these predictors (including intercept-only models for both ψ and *p*) resulted in 21 competing models. Some of these models failed to find a reliable solution (such models did not converge), and we thus removed them from the final model set. These convergence problems were presumably caused by our relatively small sample size (40 plots with three survey occasions per plot). Given that some models with one predictor variable per parameter (ψ or *p*) did not converge, we did not consider models with two or more predictors per parameter because they would certainly result in overparameterization and lack of convergence. In consequence, we were unable to examine additive or interactive effects of distinct predictor variables on occupancy or detection probabilities.

We used the Akaike Information Criterion adjusted for small samples (AICc) to choose the best-supported model (or models) for each species (Burnham and Anderson 2002). The smallest AICc indicates the model that provides the best fit to the data. We considered, however, that all the models that differed by < 2 AICc units with respect to the best-fitting model (i.e., ΔAICc < 2) also had substantial evidence in the data. Then, we used Akaike weights (*w*) as measures of the relative support for each competing model (Mazerolle 2006; Johnson and Omland 2004). Finally, we conducted model averaging with the purpose of estimating robust average values (across all plots) of occupancy and detectability for each species using all the models. Model-averaged parameter estimates consider model uncertainty and, thus, are more reliable than those derived from any single model alone (Burnham and Anderson 2002).

In addition to fitting the 21 models that resulted from all the combinations of predictor variables for *p* and ψ, we also implemented a sequential approach separately for each study species. In this sequential procedure, we began by keeping the occupancy parameter constant across plots (i.e., as an intercept-only model) while fitting the three competing models

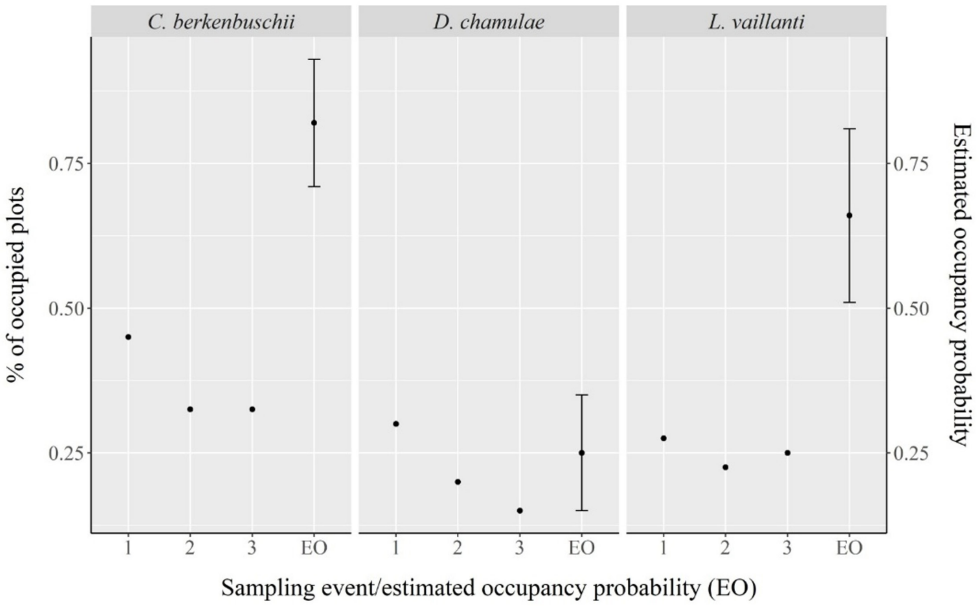

FIGURE 2. Proportion of plots where we detected Berkenbusch's Robber Frog (*Craugastor berkenbuschii*), Vaillant's Frog *(Lithobates vaillanti*), and Chamula Mountain Brook Frog (*Duellmanohyla chamulae*) in each sampling event (1, 2, and 3), and the model-averaged estimated occupancy probability across all plots (EO) ± 95% confidence interval.

that examined variation in the detection parameter (temperature, relative humidity, and an intercept-only model). We used AICc and ΔAICc < 2 to choose the best parameterization for *p*. In the next step, we used the predictor variables that we chose for *p* to fit the seven competing models that examined variation in the occupancy parameter (elevation; distance to the nearest water body; herbaceous plants; small, medium, and large trees; and an intercept-only model). Again, we used AICc and ΔAICc < 2 to choose the best parameterization for ψ. This sequential approach yielded identical model selection results as those obtained by testing all the possible combinations of the predictor variables that we used for both *p* and ψ (Appendix Table). Finally, we plotted for each species and for both parameters (occupancy and detectability) the statistical effects of the predictor variables that were included in the models with strong support in the data (models with ΔAICc < 2).

RESULTS

We found *C. berkenbuschii* in 27 plots, *L. vaillanti* in 20 plots, and *D. chamulae* in 14 plots. The proportion of occupied plots varied between species and sampling occasion (Fig. 2). *Craugastor berkenbuschii* had the highest estimated mean occupancy (EO), which was 0.82 (95% confidence interval [CI] = 0.60–1.03), followed by *L. vaillanti* with 0.66 (95% CI = 0.36–0.95) and *D. chamulae* with 0.25 (95% CI = 0.05–0.45; Fig. 2). The estimated detection probability was (maximum likelihood estimates ± standard error) 0.45 ± 0.14 for *C. berkenbuschii*, 0.38 ± 0.29 for *L. vaillanti,* and 0.72 ± 0.27 for *D. chamulae*.

The best-supported model for *C. berkenbuschii* included relative humidity as an explanatory variable for detection, whereas occupancy was not affected by any environmental variable (Table 1). Two other models, however, with substantial support included the number of small trees as an explanatory variable for occupancy (ΔAICc < 2, *w* = 0.14; Table 1). The probability of *C. berkenbuschii* occurring decreased as number of small trees in a plot increased (Fig. 3). In addition, we observed a positive relationship between relative humidity and detection probability of this species (Fig. 3).

For *L. vaillanti*, the models with strong support (ΔAICc < 2) included only explanatory variables for occupancy (medium trees: *w* = 0.22, large trees: w = 0.15, and small trees: w = 0.09), whereas detectability was not affected by any predictor variable (Table 1). Similar to what we observed for *C. berkenbuschii*, the occupancy of *L. vaillanti* decreased in plots as the number of small, medium, and large trees increased (Fig. 4). Finally, the best-fitting model for *D. chamulae* indicated elevation and temperature

Table 1. Best-supported models for occupancy (ψ) and detectability (*p*) for the Berkenbusch's Robber Frog (*Craugastor berkenbuschii*), the Vaillant's Frog *(Lithobates vaillanti*), and the Chamula Mountain Brook Frog (*Duellmanohyla chamula*), in a conserved tropical forest in Los Chimalapas region, Mexico. These competing models differ in the relationships between occupancy (ψ) and detection probability (*p*) and distinct environmental variables. For each species we only show the five models with the lowest AICc (Akaike Information Criterion for small samples) scores. Abbreviations are ΔAICc, difference between the AICc score of each model with respect to the AICc of the top model (indicated by ΔAICc = 0); *w*, Akaike weights, which are measures of the relative support for each model in the data; Hum, relative humidity; Temp, temperature; E, elevation; A1, small trees; A2, medium trees; A3, large trees. The final model for each species (i.e., the model that included the predictors with an evident influence on occupancy and detectability according to a ΔAICc < 2) is indicated with bold text.

Model	AICc	ΔAICc	*w*
C. berkenbuschii			
ψ (.) *p* (Hum)	159.22	0.00	0.31
ψ (.) *p* (.)	159.44	0.22	0.27
ψ (A1) *p* (.)	160.75	1.52	0.14
ψ (A1) *p* (Hum)	160.80	1.57	0.14
ψ (.) *p* (Temp)	161.67	2.44	0.09
ψ (A1), *p* (Hum)			
L. vaillanti			
ψ (A2) *p* (.)	134.75	0.00	0.22
ψ (A3) *p* (.)	135.44	0.69	0.15
ψ (.) *p* (.)	135.62	0.87	0.14
ψ (A1) *p* (.)	136.57	1.82	0.09
ψ (A2) *p* (Hum)	136.81	2.06	0.08
ψ (A1, A2, A3), *p* (.)			
D. chamulae			
ψ (E) *p* (Temp)	89.52	0.00	0.50
ψ (E) *p* (.)	90.53	1.00	0.30
ψ (E) *p* (Hum)	92.06	2.54	0.14
ψ (A3) *p* (Temp)	95.62	6.10	0.02
ψ (A3) *p* (.)	95.92	6.40	0.02
ψ (E), *p* (Temp)			

influenced occupancy and detection, respectively (*w* = 0.50; Table 1). A second well-supported model included an effect of elevation on occupancy, whereas detectability remained constant across sampling plots (Table 1). We detected positive relationships between *D. chamulae* occupancy and elevation (Fig. 5) and between *D. chamulae* detection probability and temperature (Fig. 5).

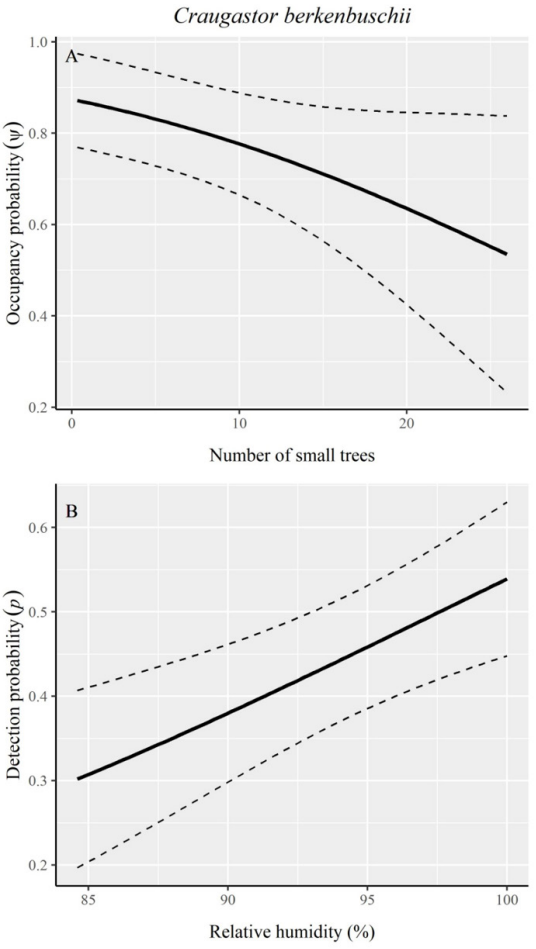

Figure 3. Occupancy and detection probabilities for the Berkenbusch's Robber Frog (*Craugastor berkenbuschii*) associated with different environmental variables: (A) occupancy probability related to the number of small trees and (B) detection probability related to relative humidity. The dotted lines correspond to ± one standard error.

Discussion

Estimated occupancy.—Anuran occupancy in the conserved tropical forest of Santa Maria Chimalapa varied among species. We did not find *C. berkenbuschii* or *L. vaillanti* at most of the sampled plots, but in both cases, the estimated occupancy (EO; 82% and 66%, respectively) was greater than the proportion of plots where we detected these species (i.e., naïve occupancy). *Craugastor berkenbuschii* has been the most abundant anuran in other community ecology studies and represents 50–80% of the total relative amphibian abundance in preserved tropical forests (Ríos-Rodas et al. 2020; Luría-Manzano et al. 2022). Despite its abundance, population trends in our region are unknown for

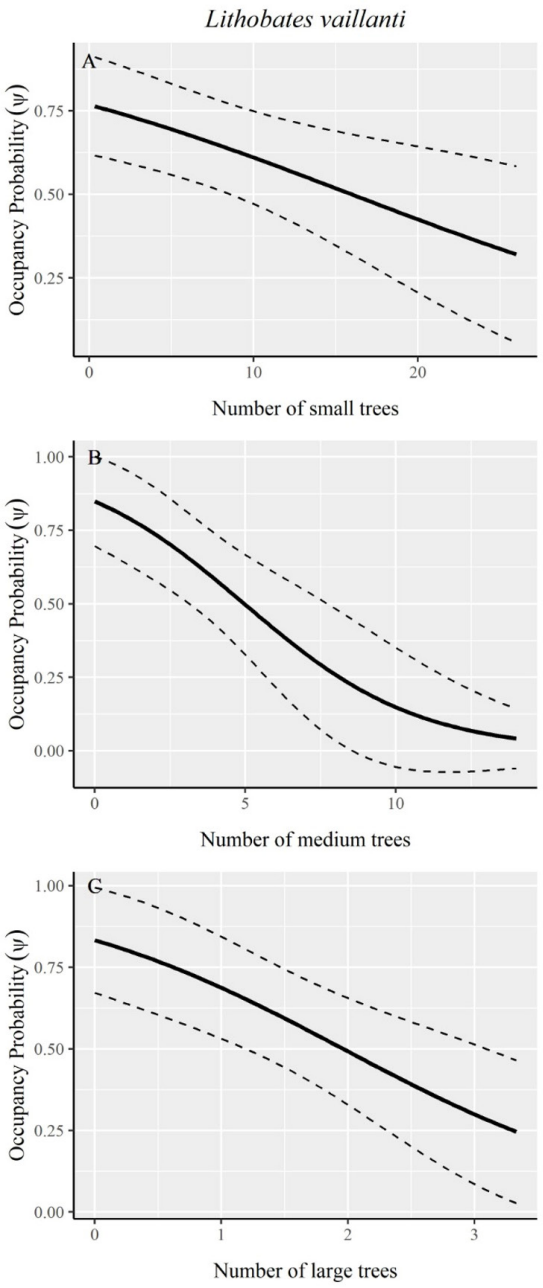

Figure 4. Occupancy probability for the Vaillant's Frog (*Lithobates vaillanti*) related to the number of (A) small trees, (B) medium trees, and (C) large trees. The dotted lines correspond to ± one standard error.

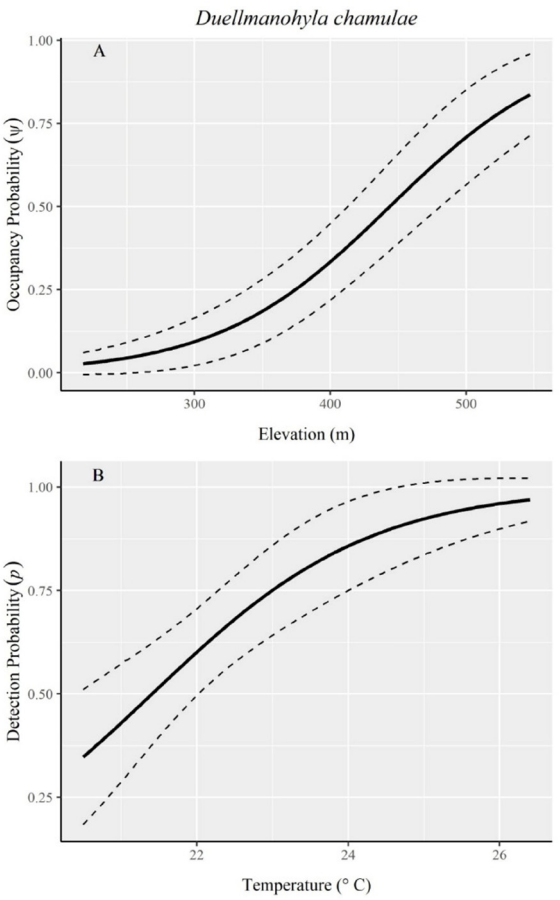

Figure 5. Occupancy and detection probabilities for the Chamula Mountain Brook Frog (*Duellmanohyla chamulae*) related to two environmental variables: (A) occupancy probability related to elevation and (B) detection probability related to temperature. The dotted lines correspond to ± one standard error.

C. berkenbuschii (IUCN ASG 2020a) and there are reports from fragmented landscapes where populations of *C. berkenbuschii* have decreased or been eliminated (Pineda and Halffter 2004; Murrieta-Galindo et al. 2013). *Craugastor berkenbuschii* is a species subject to special protection (Pr) by the Mexican government (SEMARNAT 2010) and is threatened by habitat loss and land use change (IUCN ASG 2020a). In protected areas, however, little is known about this species.

Mean occupancy of *L. vaillanti* was 66%. This species has low to intermediate abundance in preserved forests, yet other research indicates that its abundance is greater in open forests near streams (Hernández-Ordóñez et al. 2019). Given the attributes of the two sampled sites, including the high density of streams typical of preserved forests, it is unsurprising that this species was moderately common and had a high EO. This species is not threatened with extinction, and its population trend seems stable (IUCN ASG 2020b).

Estimated occupancy for *D. chamulae* (0.25) was the lowest of the three species in the two sites in the Chimalapas region. Ríos-Rodas et al. (2020) reported that this species is abundant in preserved forests, which coincides with the relative abundance that we report. Its relatively low occupancy, however, possibly was because its distribution may be

predominantly aggregated. For example, we found *D. chamulae* in few plots, but with many individuals. Additionally, this species is endangered according to the IUCN, and its population is decreasing (IUCN ASG 2020c). Additional knowledge of the natural history of *D. chamulae* is urgently needed to guide conservation plans aimed at reversing its negative population trends (IUCN ASG 2020c).

Detection.—Our results underscore the importance of detection probability as a crucial component in quantifying species occupancy. Failure to take this factor into account can result in underestimating occurrence in areas where a species is not observed (Guillera-Arroita et al. 2014). For example, detection probability varied among the species evaluated: 0.45 (± standard error) 0.14 for *C. berkenbuschii*, 0.38 ± 0.29 for *L. vaillanti*, and 0.72 ± 0.27 for *D. chamulae*. The detection probability was relatively high for *D. chamulae* and was positively influenced by increasing temperature for this species. Anurans are sensitive to environmental conditions, and very low or high temperatures can significantly reduce their activity (Duellman and Trueb 1994; Flynn et al. 2023). There are no reports about the temperature tolerance range of *D. chamulae*; however, our results indicate that the detection probability, and most likely the activity of this species, is highest at approximately 21° C. Mean detection probability of *C. berkenbuschii* was positively related to increasing relative humidity, as has been seen in other studies (Pereira-Ribeiro et al. 2019; Mason Ryan et al., unpubl. report).

Importances of environmental variables.—Our analysis revealed that the occupancy of *C. berkenbuschii* decreased as the number of small trees increased. This species is associated with streams and other water bodies despite not being directly dependent on them (IUCN ASG 2020a). It uses the space between rocks in streams as a refuge. Moreover, many of the plots where we found this species had few bushes (i.e., open understory). Some studies have shown that greater structural vegetation complexity could increase predator success due to the increase of places for predators to hide (Burrow and Maerz 2022). In tropical forests there are many species of spiders that are predators of members of the *Craugastor* genus (Luría-Manzano et al. 2022). For example, a study in La Selva, Costa Rica, revealed decreased occupancy of two anuran species where a spider of the genus *Ctenus* was also present at the sample plots. This pattern suggests that frogs avoid co-occurrence with their predators (Folt and Guyer 2021). We suggest that where small trees are abundant, there will be more litter, which in turn provides more refuge space for spiders and, consequently, fewer frogs.

Lithobates vaillanti is a semiaquatic anuran species and, like *C. berkenbuschii*, had a negative relationship with increasing tree density. This negative relationship could be because plants affect aquatic environments in different ways, including by regulating water temperature and dissolved oxygen availability. For example, water bodies with open canopies are 2–5° C warmer than those with closed canopies (Werner and Glennemeier 1999; Skelly et al. 2014; Burrow and Maerz 2022). In amphibians, temperature is associated with increases in embryonic developmental rate and larval growth rate (Brown et al. 2006). This suggests that frogs prefer open canopy plots (i.e., those with fewer trees) because such plots are warmer and therefore have better conditions for their development. Another possible explanation for the negative relationship between *L. vaillanti* occupancy and the number of trees could be that those sections of water bodies with open canopies are suitable calling places for breeding aggregations of ranids (Hamer et al. 2021).

Occupancy of *D. chamulae* increased with increasing elevation, indicating a preference for high-elevation areas. This species has an elevational range of 200–1,600 m (IUCN ASG 2020c), and it has been reported to be more abundant at high elevations (Aguilar-López et al. 2010; Ríos-Rodas et al. 2019). Thus, our records in lower areas could represent occurrences at the lower elevational limits of the species. This species inhabits mainly Cloud Forests (IUCN ASG 2020c); in Mexico, this type of vegetation occurs between 600 and 3,200 m elevation (Ochoa-Ochoa et al. 2017). Another possible explanation for this correlation could be that *D. chamulae* inhabits only preserved forests; hence, it avoids the low areas that are often correlated with human settlement patterns (Bailey et al. 2004; Cecala et al. 2018).

Relative humidity and temperature had positive relationships with the detectability of *C. berkenbuschii* and *D. chamulae*, respectively, as has been seen in other amphibian species (Pereira-Ribeiro et al. 2019; Asad et al. 2020). Amphibian activity is highly influenced by optimal ranges of temperature and relative humidity, with most anuran species increasing their activity when conditions are warmer and more humid (Preest and Pough 1989)

and, consequently, being easier for observers to detect during field surveys. Given the influence of temperature and relative humidity on the detectability of anurans in a preserved tropical forest, we suggest that these conditions be taken into account when developing monitoring activities.

Final considerations.—We provide detection and occupancy estimates for three anuran species in a preserved tropical forest, an imperiled ecosystem that is steadily decreasing at alarming rates due to deforestation for the creation of monoculture agriculture (Davis et al. 2020). Among the three study species, occupancy of *C. berkenbuschii* was highest for the region. This species is listed as subject to special protection by Mexican legislation. We also obtained important data on *D. chamulae*, which is listed as endangered, and despite having the lowest occupancy, was the species with the highest detection probability. In the case of *L. vaillanti*, although not at immediate risk, the information obtained here could serve as a baseline for the distribution of this species in a preserved tropical forest.

Additionally, we obtained valuable insights into how all these species respond to habitat conditions with respect to their distribution patterns. This information could be useful for establishing monitoring and conservation strategies for these species. The environmental variables analyzed in this study represent a small proportion of all the biotic and abiotic variables that could influence the presence of anuran species. Other environmental features that we did not measure, such as conductivity, water temperature, and the number and intensity of biotic interactions, also may have a significant influence on whether the subject species are present (or not) at a particular site. Including more environmental variables in this type of research would allow us to reach a better understanding of the site occupancy patterns of priority species.

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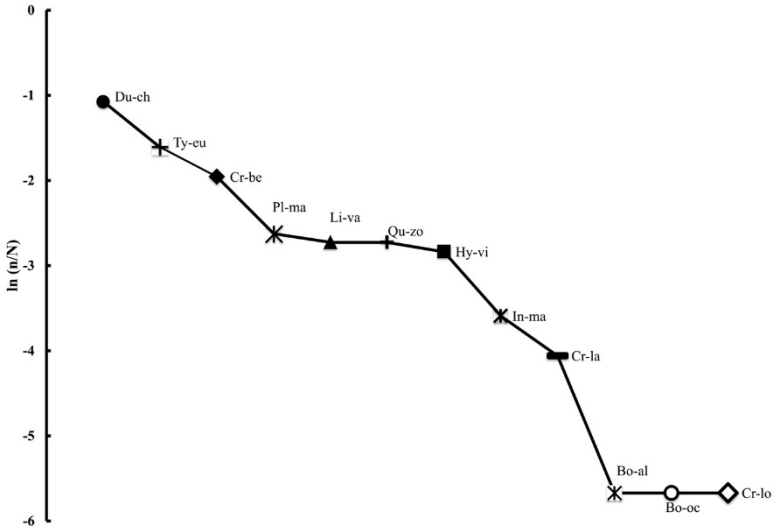
Appendix



Appendix Figure. Species rank-abundance curve for amphibian species in the Los Chimalapas region, Oaxaca, México. We found 12 species in the two surveyed localities within the preserved forest. Abbreviations are Du-ch, Chamula Mountain Brook Frog (*Duelmanohyla chamulae*); Ty-eu, Cloud Forest Stream Frog (*Ptychohyla euthysanota*); Cr-be, Berkenbusch's Robber Frog (*Craugastor berkenbuschii*); Pl-ma, Matuda's Spikethumb Frog (*Plectrohyla matudai); Li-va, Vaillant's Frog (Lithobates vaillanti*); Qu-zo, Zoque Treefrog (*Quiltychohyla zoque); Hy-vi, Northern Glassfrog (Hyalinobatrachium viridissimum*); In-ma, Large Crested Toad (*Incilius macrocristatus*); Cr-la, Broad-headed Cave Frog (*Craugastor laticeps*); Bo-al, Alberch's Salamander (*Bolitoglossa alberchi*); Bo-oc, Southern Banana Salamander (*Bolitoglossa occidentalis*); Cr-lo, Common Leaf-litter Frog (*Craugastor loki*).

Appendix Table. Model selection results from a sequential approach in which we first modeled detection probability (*p*) while keeping occupancy probability (ψ) constant across sites (i.e., as an intercept-only model) and second, we modeled the occupancy parameter using the chosen parameterization for *p*. For each species, we show first the model selection results for the detection parameter and then those for the occupancy parameter. Some models did not converge and, hence, we do not include them in this table. Abbreviations are AICc, Akaike information criterion for small samples; ΔAICc, difference between the AICc score of each model with respect to the AICc of the top model (indicated by ΔAICc = 0); *w, Akaike weights, which are measures of the relative support for each model in the data; Hum, humidity; Temp, temperature; E, elevation; A1, small trees; A2, medium trees; A3, large trees. For all three study species, this sequential approach yielded identical model selection results* as those obtained by testing all the possible combinations of the predictor variables that we used for both *p* and ψ. For each species and each parameter, we highlight in bold text the models with strongest support (ΔAICc < 2).

Species	Parameter	Model	AICc	ΔAICc	*w*
Berkenbusch's Robber Frog (*Craugastor berkenbuschii*)	*p*	ψ (.) *p* (Hum)	159.22	0.00	0.46
		ψ (.) *p* (.)	159.44	0.22	0.41
		ψ (.) *p* (Temp)	161.67	2.44	0.13
	ψ	ψ (.) *p* (Hum)	159.22	0.00	0.28
		ψ (.) *p* (.)	159.44	0.22	0.25
		ψ (A1) *p* (.)	160.75	1.52	0.17
		ψ (A1) *p* (Hum)	160.80	1.57	0.16
Vaillant's Frog (*Lithobates vaillanti*)	*p*	Ψ (.) *p* (.)	135.62	0.00	0.59
		Ψ (.) *p* (Hum)	137.60	1.97	0.22

Appendix Table, continued

Species	Parameter	Model	AICc	ΔAICc	*w*
		Ψ (.) *p* (Temp)	137.97	2.34	0.18
	Ψ	Ψ (A2) *p* (.)	134.75	0.00	0.22
		Ψ (A3) *p* (.)	135.44	0.69	0.16
		Ψ (.) *p* (.)	135.62	0.87	0.14
		Ψ (A1) *p* (.)	136.57	1.82	0.09
		Ψ (A2) *p* (Hum)	136.81	2.06	0.08
		Ψ (E) *p* (.)	136.82	2.07	0.08
		Ψ (A3) *p* (Hum)	137.51	2.75	0.06
		Ψ (H) *p* (.)	137.53	2.78	0.05
		Ψ (.) *p* (Hum)	137.60	2.85	0.05
		Ψ (A1) *p* (Hum)	138.71	3.96	0.03
		Ψ (E) *p* (Hum)	138.87	4.12	0.03
		Ψ (H) *p* (Hum)	139.73	4.98	0.02
Chamula Mountain Brook Frog (*Duellmanohyla chamulae*)	*p*	ψ (.) *p* (Temp)	103.29	0.00	0.40
		ψ (.) *p* (.)	103.29	0.00	0.40
		ψ (.) *p* (Hum)	104.76	1.47	0.19
	ψ	Ψ (E) *p* (Temp)	89.52	0.00	0.50
		Ψ (E) *p* (.)	90.53	1.00	0.30
		Ψ (E) *p* (Hum)	92.06	2.54	0.14
		Ψ (A3) *p* (Temp)	95.62	6.10	0.02
		Ψ (A3) *p* (.)	95.92	6.40	0.02
		Ψ (A3) *p* (Hum)	97.54	8.02	0.009
		Ψ (A1) *p* (.)	99.04	9.52	0.004
		Ψ (A1) *p* (Temp)	99.24	9.71	0.004
		Ψ (A1) *p* (Hum)	100.71	11.19	0.002
		Ψ (.) *p* (Temp)	103.29	13.77	0.0005
		Ψ (.) *p* (.)	103.29	13.77	0.0005
		Ψ (.) *p* (Hum)	104.76	15.24	0.0002
		Ψ (H) *p* (.)	104.82	15.30	0.0002
		Ψ (H) *p* (Temp)	104.99	15.46	0.0002
		Ψ (A2) *p* (.)	105.64	16.11	0.0001
		Ψ (A2) *p* (Temp)	105.76	16.24	0.0001
		Ψ (H) *p* (Hum)	106.44	16.92	0.0001
		Ψ (A2) *p* (Hum)	107.24	17.71	0.0001