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LONG-TERM STUDY OF OWL OCCUPANCY IN PROTECTED AREAS OF EL SALVADOR

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ABSTRACT.—Understanding patterns in the occupancy of Neotropical owls can help inform land managers and conservation efforts; however, Neotropical owls are understudied compared to their temperate kin. We conducted the first long-term (10-yr) study of owls in El Salvador to assess occurrence patterns and species richness using occupancy modeling. Our study occurred in El Imposible National Park, Montecristo National Park, and Nancuchiname Forest, and we chose two survey routes per protected area to represent the landscape diversity of the country. Surveys involved passive listening and broadcasting calls of several species at selected points along each route, and we sought to repeat each survey route twice per year. We completed 86 surveys between March and May each year from 2003 through 2013, except in 2006 when no surveys occurred. We detected nine species of owls, including the Stygian Owl (*Asio stygius*), which was previously undocumented in El Salvador, and we documented 1211 owl records overall. We developed Bayesian, hierarchical, single-species occupancy models for the Mottled Owl (*Ciccaba virgata*), Ferruginous Pygmy-Owl (*Glaucidium brasilianum*), and Spectacled Owl (*Pulsatrix perspicillata*), and a multi-species richness model for all El Salvador owls. We found that the effects of broadcasting calls were species-specific (i.e., broadcasting some species' calls increased detection probabilities while others decreased detection). Nancuchiname Forest was the most species-rich, while the cloud forest of Montecristo National Park had several species that we did not observe elsewhere. In general, we found relatively stable occupancy patterns across the study period, and we recommend some specific areas of further study to inform management decisions.

KEY WORDS: *El Salvador*; *Neotropical owls*; *occupancy modeling*; *protected areas*; *species richness.*

ESTUDIO A LARGO PLAZO DE LA OCUPACIÓN DE ÁREAS PROTEGIDAS POR ESTRIGIFORMES DE EL SALVADOR

RESUMEN.—Comprender los patrones de ocupación de los Estrigiformes neotropicales puede ayudar a informar a los administradores del territorio y a los esfuerzos de conservación; sin embargo, los Estrigiformes neotropicales son poco estudiados en comparación con sus parientes de ambientes templados. Realizamos el primer estudio a largo plazo (10 años) de búhos en El Salvador para evaluar los patrones de presencia y la riqueza de especies utilizando modelos de ocupación. Nuestro estudio se realizó en el Parque Nacional El Imposible, el Parque Nacional Montecristo y el Bosque Nancuchiname, y elegimos dos rutas de prospección por área protegida para representar la diversidad del paisaje del país. Los muestreos involucraron la escucha pasiva y la reproducción de reclamos de varias especies en puntos seleccionados a lo largo de cada ruta, y repitiendo cada ruta de muestreo dos veces al año. Completamos 86 muestreos entre marzo y mayo de cada año desde 2003 hasta 2013, excepto en 2006, cuando no se realizaron muestreos. Detectamos nueve especies de búhos, incluido *Asio stygius*, que anteriormente no estaba documentado en El Salvador, y documentamos 1211 registros de búhos en total. Desarrollamos modelos de ocupación bayesianos, jerárquicos y de una sola especie para *Ciccaba virgata*, *Glaucidium brasilianum* y *Pulsatrix perspicillata*, y un modelo de riqueza de múltiples especies para todos los búhos de El Salvador. Encontramos que los efectos de la reproducción de reclamos fueron específicos para cada especie (i.e., la reproducción de reclamos de algunas especies aumentó las probabilidades de detección mientras que otras disminuyeron la detección). El Bosque Nancuchiname fue el más rico en especies, mientras que el bosque nublado del Parque Nacional

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Montecristo tuvo varias especies que no observamos en ningún otro lugar. En general, encontramos patrones de ocupación relativamente estables durante el período de estudio, y recomendamos algunas áreas específicas de estudio adicionales para informar las decisiones de gestión.

[Traducción del equipo editorial]

Introduction

As apex predators, owls are important bioindicators of ecosystem health. Current understanding of owl ecology comes primarily from temperate systems, however (White et al. 2013, Wan et al. 2018, Buechley et al. 2019), and its applicability in the Neotropics is uncertain. The Neotropics were recently identified as a priority area for owl research because, despite their high conservation risk, past research has been insufficient to inform effective conservation of Neotropical owls (Buechley et al. 2019). That may be partly because studying owls in tropical rain and cloud forests is logistically difficult compared to studying owls in many temperate regions, despite the possibility of more diversity in the Neotropics (König et al. 1999). For this and other reasons, understanding of Neotropical owl distributions, ecological requirements, population dynamics, and reproductive behaviors is limited (Clark et al. 1978, Enríquez et al. 2006, Pérez-Léon et al. 2017, Rangel-Salazar and Enríquez 2017), which poses a challenge for proactive conservation. Although information about the status and population trends of Neotropical owls is generally limited, populations are known to be decreasing in several regions where species have been added to endangered species lists or have become locally extirpated (Enríquez et al. 2006).

The vocal patterns of nocturnal or crepuscular species can be more important than plumage for identification (König et al. 1999), and detecting vocalizations typically is the most reliable way to survey for owls (Springer 1978, Forsman 1983, Enríquez and Rangel-Salazar 2001). Knowledge of the vocalizations of tropical owls is incomplete, however, which hinders designing effective surveys in the Neotropics (König et al. 1999).

El Salvador is located in the heart of the Mesoamerican Biodiversity Hotspot on the western side of the Central American isthmus (Myers et al. 2000; Fig. 1). El Salvador is the smallest (20,721 km^2) and most densely populated country in Central America with 315 inhabitants/km^2. A majority (75%) of the land area is used for agricultural purposes and 14% is forested (Central Intelligence Agency 2021). A common agroecosystem in El Salvador is shade-grown coffee, which supports forest cover on agricultural land. Shade-grown coffee production occurs on approximately 7% of El Salvador's forested land and may provide an important land-use buffer around El Salvador's protected natural areas (Silva 2016, Pérez-Léon et al. 2017). Although shade-grown coffee systems potentially mitigate the effects of anthropogenic land uses on forest-dependent owls in El Salvador (e.g., Pérez-Léon et al. 2017), information about owls' long-term population trends is lacking. Pérez-Léon et al. (2017) identified several other human activities affecting owl populations in El Salvador, including illegal hunting, trapping, persecution, killing, and wildlife trade.

The objectives of our study were to assess owl community composition in El Salvador over the course of 10 yr to better understand patterns of owl occurrence and habitat use, and ultimately to inform future land use and management in three of El Salvador's main protected areas. We conducted nocturnal surveys with broadcast calls, and we used occupancy modeling to determine occupancy trends over the course of the study for three owl species, and species richness in these areas for all El Salvador owl species. We selected our study areas to represent the breadth of ecosystem diversity across the country and Central America. Our goal was to provide information about Neotropical owl communities that can help guide conservation in El Salvador

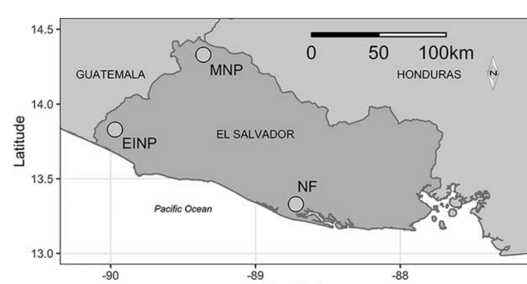

Figure 1. Locations in El Salvador where owl surveys were conducted from 2003–2013 in El Imposible National Park (EINP), Montecristo National Park (MNP), and Nancuchiname Forest (NF). Map coordinates are in decimal degrees.

Table 1. Route locations and associated land cover types where surveys were conducted for owls from 2003–2013 in three protected areas of El Salvador: El Imposible National Park (EI-1 and EI-2), Montecristo National Park (M-1 and M-2), and Nancuchiname Forest (N-1 and N-2).

ROUTE	LATITUDE (°N)	LONGITUDE (°W)	ELEVATION (masl)	LAND COVER
EI-1	13°50.75′	89°59.74′	609	Reforested deciduous forest
EI-2	13°51.38′	89°58.24′	958	Semi-deciduous forest
M-1	14°24.88′	89°21.63′	2111	Cloud forest
M-2	14°23.19′	89°22.33′	1755	Pine/oak forest
N-1	13°19.95′	88°43.63′	3	Alluvial forest with secondary growth
N-2	13°22.03′	88°43.30′	2	Alluvial forest

and throughout the region of Mesoamerican biodiversity hotspots.

METHODS

Study Areas. We conducted surveys in El Imposible National Park (NP), Montecristo NP, and Nancuchiname Forest (Fig. 1, Table 1). The three study areas were located at different elevations (low, middle, and high) and in different types of forest vegetation (alluvial, deciduous, semi-deciduous, pine-oak, and cloud forest), collectively representing a broad spectrum of the country's diverse ecosystems. We established two survey routes in each study area (Table 1).

El Imposible NP is located 119 km southwest of San Salvador. It is the largest national park in El Salvador (3792 ha), with elevations ranging from 250–1425 m above sea level (masl). Here we established one survey route (EI-1) at a lower elevation in secondary deciduous forest, and the second survey route (EI-2) higher up in semi-deciduous forest (Table 1). The terrain in this NP is steep and broken, with many cliffs (Alvarez and Komar 2003). Vegetation includes deciduous and semi-deciduous forest, secondary growth edge vegetation, and former pasture areas that were reforested with native species in 1997. More than 400 species of trees occur in the park's deciduous and broadleaf-evergreen forests, including species with buttresses, large diameters, and heights from 20–45 m. Typical large trees are *Terminalia oblonga*, *Brosimum alicastrum*, *Bursera simaruba*, *Licania retifolia*, *Manilkara chicle*, *Enterolobium cyclocarpum*, and *Ceiba pentandra* (Alvarez and Komar 2003).

Montecristo NP (1973 ha) is located 125 km northwest of San Salvador at elevations ranging from 730–2418 masl. This NP is part of the Montecristo Tri-national Protected Area, which includes extensive adjoining natural areas in Guatemala and Honduras (Komar 2010). Here we established one survey route (M-1) in high-elevation cloud forest, and a second survey route (M-2) in mid-elevation pine-oak forest that included some pine and cypress plantations (Table 1). The high-elevation cloud forest in this park is often shrouded in mist or fog, and includes abundant 20–40-m-tall canopy trees, at least 177 total tree species, and eight species of tree ferns (Komar 2002a). Canopy trees include *Quercus aaata*, *Symplocos culminicola*, *Magnolia hondurensis*, *Cornus disciflora*, and *Brunellia mexicana*; other common plant species include *Persea* spp. and *Symplocos hartwegii* (Komar 2002a, Ministerio de Medio Ambiente y Recursos Naturales 2010). The pine-oak forest contains species such as *Pinus oocarpa*, *Quercus eschineris*, *Q. tristis*, *Diphysa robinioides*, and *Perymenium grande* (Komar 2002a).

Nancuchiname Forest (797 ha) is located 95 km southeast of San Salvador. It is a protected natural area situated in the coastal alluvial plain along the Lempa River. Elevations range from sea level to 12 masl. Here we established one survey route (N-1) in alluvial forest along a dike, and a second route (N-2) in semi-deciduous alluvial forest. Nancuchiname Forest is an alluvial gallery forest that contains deciduous and semi-deciduous tree species, second-growth vegetation, native species reforestation, and a dike surrounded by secondary growth. The forest is flooded during the rainy season and is surrounded by croplands and pastures. Tree species include *Enterolobium cyclocarpum*, *Albizia caribaea*, *Matudaea trinervia*, *Andira inermis*, *Sapium macrocarpum*, *Spondias radlkoferi*, *Ceiba pentandra*, *Terminalia oblonga*, and *Quercus* spp. (Zepeda 1995, N. Pérez Romero pers. comm.). Second-growth vegetation includes grasses adjacent to the dike and shrubs and scattered trees representing various successional stages.

Survey Methods. To accomplish our surveys in study areas with limited roads, we modified standard vehicle-based roadside surveys (Takats et al. 2001) to involve surveys on foot (Fuller and Mosher 1987), and we adapted parts of a survey protocol used in Costa Rica (Enríquez and Rangel-Salazar 2001). Each of the six survey routes was 2 km long and we established 10 permanent survey points spaced at 200-m intervals in each. We marked the 60 survey points with flagging and recorded detailed vegetative descriptions, photographs in each of the four cardinal directions, elevations, and GPS coordinates.

Depending on site access and weather conditions, we attempted to conduct surveys along all routes twice per year during the breeding season (March to May) from 2003–2005 and 2007–2013. Each route survey began at local twilight and took approximately 5 hr to complete. During all surveys at each station, we recorded the current environmental conditions, including presence of precipitation; estimated cloud and fog cover; moon phase; temperature, wind speed, and barometric pressure measured using a Brunton Sherpa (Brunton Company, Riverton, WY, USA); and ambient noise level (Takats et al. 2001).

Each acoustic survey at a specific point took 12 min and consisted of passive listening for 2 min, 3 min of broadcasting owl calls, and a final 7 min of passive listening. We documented vocalizations on modified and translated (Spanish) data sheets (Takats et al. 2001). When we detected owls, we recorded the owl species, number of owls, distance and direction to the vocalizing owl, when the owl vocalized relative to the survey protocol (e.g., minute one, minute two, during broadcast, after broadcast), and observations in addition to the vocalizations (e.g., heard an owl fly overhead). After transcribing the field data, we reduced the potential for over-counting individuals by georeferencing locations and species identifications in a Geographic Information System.

To broadcast owl vocalizations, we used a Sony Walkman Sports cassette tape player (from 2002–2005 only; model WM-FS221, Sony Corp., Oradell, NJ, USA), or a Sony portable CD player (from 2007–2013; model D-NS707F, Sony Electronics Inc., San Diego, CA, USA). To amplify the broadcasts, we used a hand-held mini amplifier/speaker (Radio Shack, Fort Worth, TX, USA) with a speaker frequency response of 100–10,000 Hz, which includes the call frequency of owls. We used the recorded calls of nine different species of owls and we measured the broadcast levels with a digital VLIKE Sound Level Meter (model VL6708, Gungzhoul Like Technologies Co. Inc., Guangdong, China). At 1 m from the speaker, the sound pressure level ranged from 78–86 $\pm$ 1.5 dB, depending on the species of owl broadcast.

Whenever possible, we used owl vocalizations recorded locally to maximize owl responses (Gerhardt 1989), and we recorded owl vocalizations throughout the study for species verification and to add to the knowledge of owl vocalizations in the country. If an owl closely approached the broadcast speaker during a survey and vocalized, we stopped broadcasting and recorded the owl's vocalization using a professional cassette recorder, an omnidirectional microphone, and a parabolic sensor.

We broadcast the same suite of species-specific owl calls along the routes in El Imposible NP and Nancuchiname Forest, but we represented a different suite of species in Montecristo NP to reflect the change in vegetation and distribution of owl species at higher elevations. Throughout the study, we always broadcast calls of only one species at each individual survey point. Along all routes in El Imposible NP (EI-1 and EI-2) and Nancuchiname Forest (N-1 and N-2), we broadcast vocalizations of five species in the following sequential order across survey points 1–10: Pacific Screech-Owl (*Megascops cooperi*), Mottled Owl (*Ciccaba virgata*), Crested Owl (*Lophostrix cristata*), Black-and-white Owl (*C. nigrolineata*), Spectacled Owl (*Pulsatrix perspicillata*), Pacific Screech-Owl, Mottled Owl, Crested Owl, Black-and-white Owl, and Spectacled Owl. Across the 10 survey points along the two routes in Montecristo NP (M-1 and M-2), we broadcast vocalizations of five species in the following sequential order: Whiskered Screech-Owl (*Megascops trichopsis*), Mottled Owl, Fulvous Owl (*Strix fulvescens*), Stygian Owl (*Asio stygius*), Great Horned Owl (*Bubo virginianus*), Whiskered Screech-Owl, Mottled Owl, Fulvous Owl, Stygian Owl, and Great Horned Owl.

Single-species Occupancy Model. We modeled occupancy within each route, year, and survey assuming that the probability of occupancy would be closed across surveys of a given route in a given year. In other words, for any single species of owl, we assumed that the probability of a route being occupied would not change between surveys within a year but could vary among years. We applied a hierarchical occupancy model in which the probability of detecting an owl depended on both the owl being present and the probability of detecting that owl given the call broadcast at a given survey station. We built this model with a Bayesian framework in JAGS; full modeling details are provided as Supplemental Material. We also archived the complete data

Table 2. Species detection records by route and vocalizations recorded during owl surveys conducted from 2003–2013 in three protected areas in El Salvador: El Imposible National Park (EI-1 and EI-2), Montecristo National Park (M-1 and M-2), and Nancuchiname Forest (N-1 and N-2).

Species	Survey Route					
	EI-1	EI-2	M-1	M-2	N-1	N-2
Barn Owl (*Tyto alba*)[a]	0	0	0	0	8	2
Whiskered Screech-Owl[ab]	0	0	0	2	0	0
Pacific Screech-Owl[a]	11	1	0	0	6	9
Spectacled Owl[ac]	1	1	0	1	59	75
Great Horned Owl[a]	0	0	3	0	0	0
Ferruginous Pygmy-Owl[a]	4	0	0	0	82	98
Mottled Owl[a]	214	117	1	22	62	114
Fulvous Owl[ac]	0	0	17	0	0	0
Stygian Owl	0	0	0	1	0	0

[a] Vocalizations recorded.
[b] Threatened species (Ministerio de Medio Ambiente y Recursos Naturales 2015).
[c] Endangered species (Ministerio de Medio Ambiente y Recursos Naturales 2015).

and code necessary to replicate our results in the curated data repository for the University of Minnesota (Archer and West 2021).

Briefly, we assumed that the probability of occupancy during each survey was the outcome of Bernoulli trials that we allowed to vary by year and route. Further, we assumed that detecting an owl depended on it being present during that survey and the probability of detection, which was related to the species-specific broadcast call. This model provided a consistent probability of detection for all surveys in the first 2 min of each observation period before calls were broadcast. The probability of detection for each post-broadcast period then depended on which species' call had been broadcast. This combination enabled consideration of species-specific behaviors in response to different broadcast calls (Baumgardt et al. 2019). We used means parameterization to develop a logistic regression model with coefficients that could be interpreted as representing the effect of either the pre-broadcast period or the specific broadcast call on the probability of detection.

We developed single-species occupancy models for three owl species that had sufficient detections for analysis: Mottled Owl, Spectacled Owl, and Ferruginous Pygmy-Owl (*Glaucidium brasilianum*; Table 2). We based our threshold for sufficient data on the degrees of freedom spending approach described by Giudice et al. (2012). In this case, our detection model included 10 predictor levels and, therefore, was based on nine degrees of freedom, which translated to a need for at least 90 detections per species to support effective modeling. However, we also wanted to provide additional degrees of freedom for the hierarchical occupancy model. The predictor levels and hierarchical framework together ideally required at least 120 detections for each single-species occupancy model. Further, based on our understanding of owl ecology, we assumed that Spectacled Owls and Ferruginous Pygmy-Owls would not occupy route M-1 in Montecristo, so we removed M-1 from those species' occupancy analyses.

We used the *R2jags* package in R (Plummer 2017, R Core Team 2017) to implement the single-species occupancy models. For each model, we ran three chains for 10,000 iterations and discarded 1000 iterations as burn-in, for a total of 27,000 iterations composing the posterior distributions for each model parameter. We verified that $\hat{R}$s were lower than 1.3 and visually inspected traceplots to verify that chains mixed well. After analysis, we also used logistic regression to determine whether median probabilities of occupancy were affected by time for each route and species. We based our evaluation of significance on a threshold value of $P < 0.10$.

Richness Model. To model species richness, we assumed there were 14 possible owl species present in El Salvador. This included the nine species observed during our surveys (Table 2) and an additional five species that we did not observe but have been documented for El Salvador (i.e., Crested Owl, Burrowing Owl [*Athene cunicularia*], Black-and-white Owl [endangered], Striped Owl [*Asio clamator*], and Unspotted Saw-whet Owl [*Aegolius ridgwayi*]). This upper limit to expected species richness derived from the 13 species previously known to inhabit El Salvador (Pérez-Léon et al. 2017), plus one species we confirmed that had not previously been documented in the country (Stygian Owl). Thus, we augmented our owl detection data with five additional potential species for which we recorded zero detections (Royle et al. 2007).

We assumed that estimated species richness along a given route during an individual annual survey depended on both the probability of a given species belonging to that route's community and the probability of occupancy for that survey, route, and year. To share information about occupancy among species, we incorporated random effects in the model, such that the probability of occupancy for each species, route, and year was drawn from one average probability of occupancy for each route and year (see Supplemental Material for parameterization details; Guillera-Arroita et al. 2019). We then calculated route-level species richness as the sum of owl species present on each route and calculated annual richness similarly by route and year.

Consistent with our approach for occupancy models, we assumed that detecting an owl depended on an individual of that species being present during that survey and the species-specific probability of detection, which was related to the broadcast call. The coefficients of the detection model were assumed to be consistent for all owl species, which allowed us to borrow information about the detection process for undetected owl species from those that were detected.

We used the *R2jags* package to implement the richness models. We ran three chains for 20,000 iterations with 2000 iterations discarded as burn-in and a thinning rate of two, for a total of 27,000 iterations composing the posterior distributions for each model parameter. We verified that $\hat{R}$s were lower than 1.3 and visually inspected traceplots to verify that chains mixed well. We based our evaluation of significance on a threshold value of $P < 0.10$ and present all modeled estimates as median values with 90% credible intervals.

Results

We conducted 86 surveys across the 10-yr study. We made 1211 owl detections in the three study areas, comprising 911 detections during standardized surveys, 163 detections documented incidentally along survey routes and noted on survey forms, and 137 detections recorded elsewhere in the study areas and documented in field notes. We detected nine species of owls (Table 2). In Montecristo NP, we documented Whiskered Screech-Owls, where they had not been confirmed before, and identified a Stygian Owl, which had not previously been confirmed in El Salvador.

Single-species Occupancy Models. For Mottled Owls, Spectacled Owls, and Ferruginous Pygmy-Owls, we recorded 530, 137, and 184 detections, respectively, during the standardized surveys only (Table 2). For all other species together, we recorded 60 detections during the standardized surveys, which precluded developing other species-specific occupancy models.

Large credible intervals prevented us from making statistical conclusions about patterns in the probability of occupancy over time for any route or owl species. However, averaged across years, the probability of occupancy was lowest for Mottled Owls along route M-1 in Montecristo NP (Fig. 2). The median probability of occupancy along the EI-1 and EI-2 routes in El Imposible NP was 0.84 (0.30, 0.99) and 0.85 (0.31, 0.99), respectively. The probability of occupancy along the N-1 and N-2 routes in Nancuchiname Forest was 0.73 (0.09, 0.98) and 0.84 (0.30, 0.99), respectively. In contrast, the probability of occupancy along the M-1 and M-2 routes in Montecristo NP was 0.26 (0.01, 0.94) and 0.69 (0.04, 0.98), respectively. The estimated annual probabilities of occupancy for Mottled Owls showed

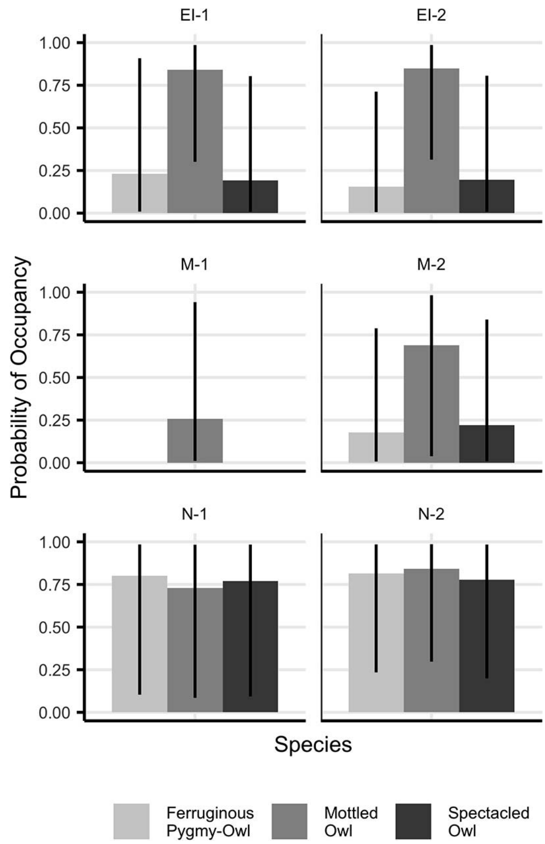

Figure 2. Probability of occupancy summarized by route for Ferruginous Pygmy-Owls, Mottled Owls, and Spectacled Owls detected during surveys conducted from 2003–2013 in El Salvador in El Imposible National Park (survey routes EI-1 and EI-2), Montecristo National Park (M-1 and M-2), and Nancuchiname Forest (N-1 and N-2). Posterior probabilities are represented as medians ± 90% credible intervals.

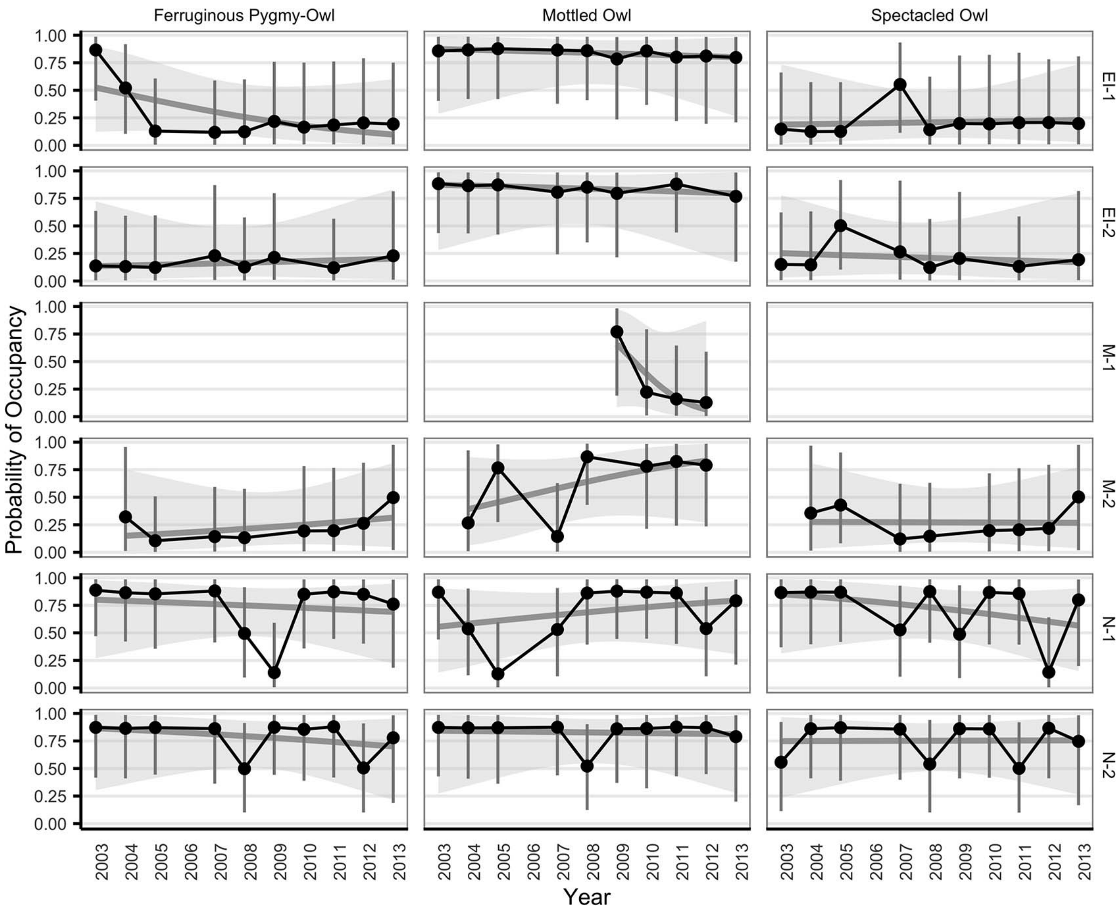

Figure 3. Probability of occupancy by route and year for Ferruginous Pygmy-Owls, Mottled Owls, and Spectacled Owls detected during surveys conducted from 2003–2013 in El Salvador: El Imposible National Park (survey routes EI-1 and EI-2), Montecristo National Park (M-1 and M-2) and Nancuchiname Forest (N-1 and N-2). Posterior probabilities are represented as medians (black dots) ± 90% credible intervals (gray vertical error bars). Results of logistic regression of median probabilities of occupancy versus time are represented with gray trend lines and light gray shading (90% confidence bands).

no significant trends across years of the study ($P >$ 0.10 for all routes; Fig. 3).

The median probability of occupancy for Ferruginous Pygmy-Owls averaged higher along the two routes in Nancuchiname Forest than along the two routes in El Imposible NP and route M-2 in Montecristo NP (Fig. 2). The probability of occupancy along routes N-1 and N-2 was 0.80 (0.10, 0.98) and 0.81 (0.23, 0.98), respectively. In contrast, the probability of occupancy along the EI-1 and EI-2 routes was 0.23 (0.01, 0.91) and 0.16 (0.01, 0.71), respectively, and the probability of occupancy along the M-2 route was 0.18 (0.01, 0.79). Similar to Mottled Owls, the estimated annual probabilities of occupancy for Ferruginous Pygmy-Owls showed no significant trends across years of the study ($P > 0.10$ for all routes; Fig. 3).

The results for Spectacled Owls and Ferruginous Pygmy-Owls were similar, averaging higher along the two Nancuchiname Forest routes than along the two El Imposible NP routes and the M-2 route in Montecristo NP (Fig. 2). The probability of occupancy for Spectacled Owls along routes N-1 and N-2 was 0.77 (0.09, 0.98) and 0.78 (0.20, 0.98), respectively. In contrast, the probability of occupancy along routes EI-1 and EI-2 was only 0.19 (0.01,

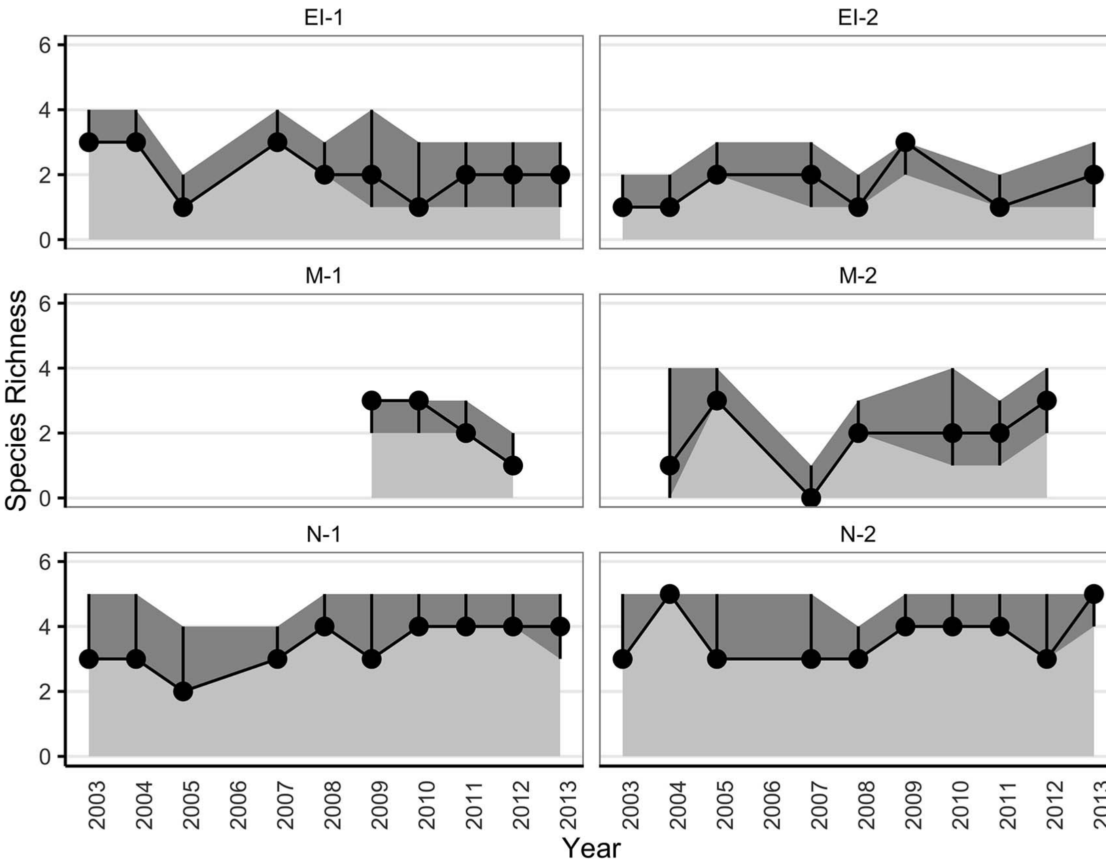

Figure 4. Species richness by route and year derived from owl surveys conducted from 2003–2013 in El Salvador in El Imposible National Park (survey routes EI-1 and EI-2), Montecristo National Park (M-1 and M-2), and Nancuchiname Forest (N-1 and N-2). Posterior probabilities are represented as medians (black dots) ± 90% credible intervals (dark gray shading and vertical black lines). Light gray shading represents the numbers of owl species detected along each survey route in each year.

0.80) and 0.20 (0.01, 0.81), respectively, and probability of occupancy along route M-2 was 0.22 (0.01, 0.84). Just as for the other two focal species, the estimated annual probabilities of occupancy for Spectacled Owls showed no significant trends across years of the study ($P > 0.10$ for all routes; Fig. 3).

Richness Models. When analyzed by year and route, estimated median species richness varied from 0–5 (Fig. 4). Along both El Imposible NP routes, median species richness ranged from 1 to 3. The 90% credible intervals added at most three species in addition to those detected in EI-1 (i.e., in 2009) and two species in addition to those detected in EI-2 (i.e., in 2007). In Montecristo NP routes M-1 and M-2, median species richness ranged from 0 to 3, and credible intervals added at most one and four additional species in routes M-1 and M-2, respectively. In Nancuchiname Forest, median species richness peaked at four species in route N-1 and five species in route N-2. At most, the credible intervals added an additional two species to these two routes.

Probability of Detection. Including all detected species in one richness model did not change the interpretation of the effects of broadcast calls on detection probability compared to results from the Mottled Owl single-species occupancy model (i.e., compare "All Species" with individual species' occupancy model results in Fig. 5). Based on the integrated all-species model, broadcasting calls of Mottled Owls, Pacific Screech-Owls, Crested Owls, Black-and-white Owls, and Spectacled Owls increased the probability of detection

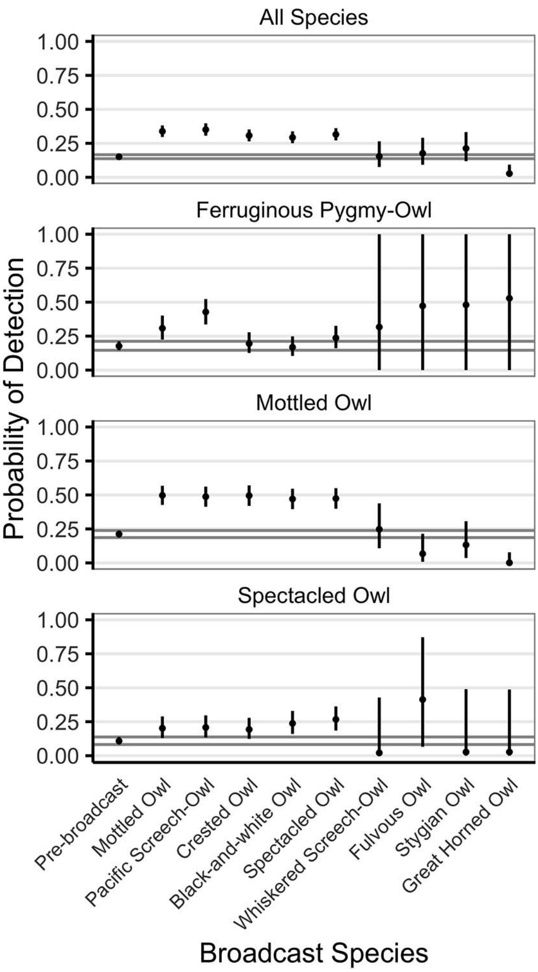

Figure 5. Probabilities of detecting owls before and after broadcasting vocalizations along survey routes from 2003–2013 in three protected natural areas of El Salvador, in relation to the species whose calls were broadcast. Logistic regression coefficients were derived from a species richness model that combined all detected species (All Species), and from single-species occupancy models for Ferruginous Pygmy-Owls, Mottled Owls, and Spectacled Owls. Posterior probabilities are represented as medians (black dots) ± 90% credible intervals (vertical black bars), and credible intervals for pre-broadcast effect sizes are represented as two gray horizontal lines on each graph.

compared to the pre-broadcast period, broadcasting Great Horned Owl calls decreased the probability of detection, and broadcasting calls of Whiskered Screech-Owls, Fulvous Owls, and Stygian Owls did not alter the probability of detection significantly.

When analyzed as single-species occupancy models, broadcasting calls significantly influenced the probability of detection for Ferruginous Pygmy-Owls, Mottled Owls, and Spectacled Owls, and the responses of all three species varied significantly depending on the call species we broadcast (Fig. 5). The results for the Mottled Owl, the most commonly detected species, mirrored those of the all-species model. In contrast, the probability of detecting Ferruginous Pygmy-Owls increased significantly only after broadcasting calls of Mottled Owl and Pacific Screech-Owl, and never decreased below the pre-broadcast value in response to any of the broadcast calls. Similarly, the probability of detecting Spectacled Owls increased significantly only after broadcasting calls of Pacific Screech-Owl, Black-and-white Owl, and Spectacled Owl, and no significant effects were evident for any of the other call species we broadcast.

DISCUSSION

We were not always able to achieve our ideal sampling objective because of issues with site access, as well as poor weather, which decreases owl vocalizations and detections (Takats et al. 2001, Andersen 2007). Nevertheless, our surveys yielded sufficient data to analyze occupancy patterns for three species of interest—Mottled Owl, Ferruginous Pygmy-Owl, and Spectacled Owl—and to estimate owl species richness by route and year.

Mottled Owls were the most frequently detected species during our surveys. They are the most common and widespread large owl in Central America (Vallely and Dyer 2018), and they have been documented across a wide range of habitats and elevations in Mexico (Enríquez-Rocha et al. 1993). Dickey and van Rossem (1938) considered Mottled Owls to be forest owls that frequented the thickest parts of forests both day and night. While the probability of occupancy for all routes was relatively high for Mottled Owls, most of the individuals that we observed in this study were in primary forest and, to a lesser degree, in coffee plantations in the western portion of El Imposible NP during 1979–1981 (West 1988). A recent study indicated that Mottled Owl populations in El Salvador have persisted despite habitat loss that has restricted the distribution of several other owl species (Pérez-Léon et al. 2017). In contrast, Mottled Owl populations in La Selva, Costa Rica, may have decreased during the past 30 yr (Enríquez and Rangel-Salazar 2001). Our results indicated that

Mottled Owls are still relatively common in each of our study areas; however, the declining trend in median probabilities of occupancy for Mottled Owls on route M-1 from 2009 to 2013 suggests that further study of this owl in Montecristo NP may be warranted.

We recorded multiple vocalizations for all detected species except Stygian Owl. The most common Mottled Owl vocalizations (uttered by both males and females) were territorial calls consisting of 2–3 lower-volume, muffled, secondary hoots, followed by three separated primary hoots. Variation in hoot sequences allowed us to identify individual Mottled Owls, and we could distinguish female territorial vocalizations as higher pitched than male vocalizations. The cat-like yowls given by females (food solicitation calls) were also frequently heard. The Mottled Owl vocalizations we heard matched the descriptions of vocalizations in Tikal NP, Guatemala (Gerhardt and Gerhardt 2012). Because these calls were easily distinguished, we believe that future studies could use individual call patterns and acoustic spectrogram analysis (e.g., Wood et al. 2019) to better understand Mottled Owl species abundance and microhabitat use in these forests.

Ferruginous Pygmy-Owl was the second-most frequently detected species in our study, commonly vocalizing closer to sunset rather than later in the evening. However, they exhibited relatively low occupancy rates in El Imposible NP and on the M-2 route in Montecristo NP. These owls tend to prefer open cover types with a lot of edge habitat, such as the flooded *igapó* forests of Amazonia (Borges et al. 2004) and heterogenous forests in central Argentina (Campioni et al. 2013). Furthermore, the diet of Ferruginous Pygmy-Owls varies based on forest density (Sarasola and Santillán 2014). Lower elevation areas in the western portion of El Imposible NP were grazed and dotted with houses in the early 1980s, and this mixed agrarian landscape may have provided an abundance of suitable forest-edge habitat for Ferruginous Pygmy-Owls. However, subsequent vegetation changes and reforestation in 1997 later reduced the availability of such habitat in this area. Thus, the abundance of Ferruginous Pygmy-Owls may have diminished in some areas as the availability of forest edge habitat declined in El Salvador, and further study may be warranted to develop a better understanding of how this species responds to vegetation management. Poaching also may be a risk factor for these owls; of eight species of owls confiscated from local markets from 1995–2008, Mottled Owls and Ferruginous Pygmy-Owls were the most common (Pérez-Léon et al. 2017), likely because they are the most widely distributed and common species in Neotropical environments.

Spectacled Owls followed similar occupancy patterns as Ferruginous Pygmy-Owls, with highest occupancy in the alluvial Nancuchiname Forest. Spectacled Owls can be found in a range of forest types and land uses, including coffee plantations and urban parks (Marín-Gómez et al. 2017), and they tend to prefer lowland forests below 1000 masl (Enríquez-Rocha et al. 1993, Orihuela-Torres et al. 2018). In a previous study from 1979–1981, we observed Spectacled Owls in the western portion of El Imposible NP at lower elevations in primary forest near El Imposible River and its small tributaries (West 1988). In this study, we detected Spectacled Owls along each of the routes located at low to moderate elevations, as well as in Montecristo NP at 1755 masl, which may be near the maximum of the species' elevation tolerance. Spectacled Owls reportedly prefer mammalian prey over reptiles and arthropods (Orihuela-Torres et al. 2018), and preferentially hunt near fallen logs where small mammals often seek refuge (Esclarski and Cintra 2014). Further study of Spectacled Owl habitat selection would improve understanding of their ecology and distribution in the Neotropics, and specifically in El Salvador.

As in our study, a recent study in Mexico found maximum owl species richness of five species, including Mottled Owls, Black-and-white Owls, Spectacled Owls, Crested Owls, and Middle American Screech-Owls (*Megascops guatemalae*; Rivera-Rivera et al. 2012). Nancuchiname Forest was the richest in owl diversity of the three protected areas we studied; however, the Nancuchiname Forest Management Plan (Zepeda 1995) listed only the Ferruginous Pygmy-Owl as occurring in the forest. In addition, although Nancuchiname Forest had the highest estimated richness, we detected four owl species only in Montecristo NP: Whiskered Screech-Owl, Great Horned Owl, Fulvous Owl, and Stygian Owl. Fulvous Owls and Stygian Owls are considered habitat specialists, whereas Whiskered Screech-Owls and Great Horned Owls are considered forest generalists and habitat generalists, respectively (Pérez-León et al. 2017). Fulvous Owls are one of El Salvador's 18 endemic bird species (Komar 2002b), and we detected them numerous times in the cloud forest of Montecristo NP along route M-1.

A Fulvous Owl was also recently photographed in Montecristo NP (Gonzalez et al. 2017).

Stygian Owls, which often inhabit dense cloud forests at elevations ranging from 1500–3000 masl (Enríquez-Rocha et al. 1993), were listed as an owl species expected to reside in El Salvador (Pérez-Léon et al. 2017), but they had not been previously detected in the country. On 26 March 2002, after listening to recordings and viewing photographs, the Montecristo NP park staff thought Stygian Owls were present in the park. Although we detected only one Stygian Owl during our standard surveys on 21 March 2005, we also heard Stygian Owl calls along route M-2 between different survey points twice on 20 March 2005 and once on 25 April 2007. We did not record any of these vocalizations, and detections that occurred between stations or away from survey routes were not included in our analyses. Thus, while we are confident that Stygian Owls inhabit Montecristo NP, further documentation is necessary to understand this species' distribution and abundance in El Salvador.

West (1988) detected six species of owls from 1979–1981 in the western portion of El Imposible NP, including two species that we did not detect in El Imposible NP: Barn Owl (*Tyto alba*) and Black-and-white Owl. In 2002, Barn Owls were detected in a cave on Loma de Paja Mountain, which is on the other side of the ridge from this study's routes in El Imposible NP (V. Campos Aguirre pers. comm.). NP staff also indicated that Black-and-white Owls were observed in two areas of the Mistepe River Valley in 2002. Thus, though we did not detect them during our surveys, these two owl species likely still occur in El Imposible NP.

Globally, an estimated 75% of nearly 250 species of owls are associated with dense, undisturbed forests (Mikkola 2012). Like many forest-dependent owl species, Neotropical owls are difficult to survey due to their cryptic nature and nocturnal habits. Visual identifications are relatively rare, and many owl surveys rely on aural detections. Distinguishing individuals by noninvasive means, such as vocal traits, is also preferable when species are rare, sensitive to handling, elusive, or when other techniques are infeasible (Terry et al. 2005). Owls vocalize to communicate with the same species, to threaten or provoke other species, and to delimit territory (Johnsgard 2002). Our surveys involved periods of passive listening followed by broadcasting vocalizations designed to trigger vocalization from owls as a means of increasing the probability of detection. Overall, the probability of detection was lower during passive listening periods before broadcast than after playing vocalizations, although the specific effect of each call varied by species.

Owls are sensitive to interactions with other owls (Enríquez and Rangel-Salazar 1997, Baumgardt et al. 2019) and may change their response to broadcast calls depending on their life stage (e.g., courtship vs. caring for nestlings; Flesch and Steidl 2007). We found that owl species varied in their responsiveness to intra- and inter-specific broadcast vocalizations, which influenced the probability of detection for multiple species in our study system. We recommend that future studies targeting Neotropical owls take this into account. Specifically, our study supports using vocalizations from Mottled Owls, Pacific Screech-Owls, Crested Owls, Black-and-white Owls, and Spectacled Owls to increase detection rates in similar Neotropical areas. In contrast, our results do not support using vocalizations of Whiskered Screech-Owls, Fulvous Owls, Stygian Owls, or Great Horned Owls to increase detection rates of Neotropical owls. Further monitoring that combines vocalizations from owls that triggered detections in our study with acoustic spectrogram analysis (e.g., Wood et al. 2019) may provide future researchers with more definitive species-richness estimates to better understand the distribution of owls in these diverse forest habitats.

We estimated owl species richness to be 3–5 species across the protected areas of our study, which were all relatively intact natural areas. We found no significant changes in occupancy over time (11 yr) for any species or route, other than a possible (nonsignificant) decrease in Mottled Owl occupancy in the montane cloud forest of Montecristo NP. Another recent study also reported that natural ecosystems in El Salvador, such as the cloud forest and deciduous, riparian, and pine-oak forests similar to those in our study, had the most diverse owl populations (Pérez-Léon et al. 2017). These results demonstrate the importance of maintaining protected areas, natural forested areas, and land-cover heterogeneity to sustain biodiversity that includes diverse owl communities in a country and region that is experiencing considerable developmental pressures.

Supplemental Material (available online). Complete modeling framework for the single-species occupancy and richness models, including assumptions, prior distributions, and parameterization.

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