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OWL OCCURRENCE AND CALLING BEHAVIOR IN A TROPICAL RAIN FOREST

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ABSTRACT.—We estimated owl occurrence (number of individuals per km of trail/night) from spontaneous calls and responses to broadcast vocalizations, during 12 repetitions of each method over 3 2-km trails from April–September 1995 at La Selva Biological Station, Costa Rica. We found Vermiculated Screech-Owls (*Otus vermiculatus*, 0.75 owls/km) and Crested Owls (*Lophostrix cristata*, 1.42 owls/km) to be common, and Mottled Owls (*Strix virgata*, 0.32 owls/km) and Black-and-white Owls (*S. nigrolineata*, 0.10 owls/km) to be uncommon. Spectacled Owls (*Pulsatrix perspicillata*, 0.06 owls/km) and Central American Pygmy-Owls (*Glaucidium griseiceps*, 0.03 owls/km) were rare. When compared to earlier reports, our results suggested that owl occurrence has changed in recent years at La Selva Biological Station. Broadcast vocalizations significantly increased the detections of only Mottled Owls. Detections of all species increased when illumination was less, although this was statistically significant only for Crested and Mottled Owls. Three species were significantly associated with moon phase. Owl detections tended to be greater during darker periods when the moon was approximately full (either before moon rise or due to cloud cover). Significantly more Vermiculated Screech-Owls were detected away from the summer solstice, while significantly fewer Crested Owls and Spectacled Owls were detected away from the solstice. Detections decreased with time after official sunset, although this was statistically significant only for Spectacled Owls. Our results suggested that changes in owl calling activity was correlated with other species activity, the season of the year, and environmental conditions.

KEY WORDS: *Vermiculated Screech-Owl*; Otus vermiculatus; *Crested Owl*; Lophostrix cristata; *Mottled Owl*; Strix virgata; *Black-and-white Owl*; Strix nigrolineata; *Central American Pygmy-Owl*; Glaucidium griseiceps; *Spectacled Owl*; Pulsatrix perspicillata; *vocalizations*; *tropical forests*; *Costa Rica.*

Ocurrencia de Búhos y Comportamiento del Llamado en un Bosque Tropical Lluvioso

RESUMEN.—Estimamos la ocurrencia de búhos (número de individuos por km de transecto por noche) por medio de dos métodos, llamados espontáneos y provocación auditíva, con 12 repeticiones por cada método en 3 transectos de 2 km cada uno, en La Estación Biológica La Selva, Costa Rica de abril a septiembre de 1995. *Otus vermiculatus* (llamados 0.75 búhos/km y respuestas 0.89 búhos/km) y *Lophostrix cristata* (1.42 y 1.39) fueron especies comunes, *Strix virgata* (0.32 y 0.71) y *S. nigrolineata* (0.10 y 0.19) fueron poco comunes, y *Pulsatrix perspicillata* (0.06 y 0.03) y *Glaucidium grisceiceps* (0.03 y 0.04) fueron especies raras. Cuando realizamos comparaciones con reportes previos de ocurrencia de búhos en La Selva, nuestros resultados sugieren que esta ocurrencia ha estado cambiando en La Selva. El método de provocación auditíva incrementó significativamente las detecciones solo para *S. virgata*. Las detecciones vocales de todas las especies incrementaron cuando la iluminación disminuyó, aunque fue significativa solo para *L. cristata* y *S. virgata*. Las vocalizaciones de tres especies estuvieron asociadas significativamente con la fase lunar. La detección de los búhos incrementó durante períodos obscuros en días cercanos a luna llena (antes que la luna saliera o en días nublados). Por otro lado, *O. vermiculatus* fue significativamente detectado más en días lejanos al solsticio de verano, mientras que *L. cristata* y *P. perspicillata* fueron detectados más en días cercanos al solsticio de verano. Las detecciones de las especies de búhos decrecieron con el tiempo después del atardecer. Nuestros resultados sugieren cambios en las poblaciones de búhos y que la actividad vocal esta correlacionada con la actividad de otras especies, temporada y ciertas condiciones ambiental.

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Table 1. Mean owl occurrence for six owl species at La Selva Biological Station, Costa Rica, per km of trail/night and total occurrences counted for spontaneous calls and responses to call broadcasts over 12 repetitions on three 2-km trails from April–September 1995.

	METHOD					
	CALLING		RESPONSES			
SPECIES	OWLS/km	TOTAL	OWLS/km	TOTAL	D[1]	*P*
Vermiculated Screech-Owl	0.75	54	0.89	65	0.866	0.45
Crested Owl	1.42	103	1.39	100	0.57	0.89
Spectacled Owl	0.06	4	0.03	2	1.15	0.14
Central American Pygmy-Owl	0.03	3	0.04	3	1.15	0.14
Mottled Owl	0.32	23	0.71	47	1.44	0.03
Black-and-white Owl	0.10	7	0.19	14	0.86	0.45

[1] Kolmogorov-Smirnov two-sample test.

An understanding of the dynamics of raptor populations is fundamental in their conservation (Newton 1979, Thiollay 1989). However, limited population data exist for owls (Mikkola 1992). Most species of owls inhabit tropical forests, but we know very little about their natural history and ecology (Clark et al. 1978, Newton 1979, Mikkola 1992). Indeed, further study is essential for their conservation in tropical areas where forests are declining.

Most owl species are active at night; therefore, it is easier to hear than see them, and counting their vocalizations has generally been the most reliable way of detecting them (Springer 1978, Forsman 1983, Smith 1987). Two methods based on vocalizations have commonly been used to survey and estimate occurrence and densities of nocturnal birds of prey. The first method is based on counts of spontaneously given calls (spontaneous calling) by owls and the second method uses counts of responses by owls to tape-recorded playbacks (Fuller and Mosher 1981, Marion et al. 1981, Mosher et al. 1990). Both methods have been used extensively in surveys of single species in temperate habitats (Smith et al. 1987, Mosher et al. 1990), but rarely in tropical forests for tropical species of owls (Gerhardt 1991).

Tropical rain forests surrounding La Selva Biological Station in Costa Rica have come under increasing pressure from people in recent years (Braker and Greene 1994, McDade et al. 1994), and the negative impacts have resulted in declines in some bird populations (Levey and Stiles 1994). To enable documentation of future declines in owl populations, we conducted research to develop a standardized method of detecting the occurrence of owl species at La Selva Biological Station by comparing the two methods used to estimate owl occurrence and to identify the environmental factors that might influence owl vocal activity.

STUDY AREA AND METHODS

La Selva Biological Station is located in Sarapiqui County, Heredia Province, Costa Rica (10°26′N, 83°59′W). La Selva adjoins Braulio Carrillo National Park to the south and borders agricultural and pastureland to the north. The station covers 1513 ha at the ecotone between tropical premontane and very humid tropical forest life zones (Hartshorn 1983). Elevations range from 35–150 m. Weather conditions are very humid with 4000–4500 mm of annual rainfall, most of which falls in June–July, and November–December. Although there is no pronounced dry season, less rain falls from February through April. March is the driest month of the year, August the warmest (mean temperature = 27.1°C), and January the coldest (mean temperature = 24.7°C) (McDade et al. 1994).

We estimated the occurrence of owl species by recording spontaneous calling and responses to playback of owl calls. Thirty permanent survey stations were spread at 200-m intervals over 3 2-km trails (10 stations per trail) Each station was surveyed on 24 different nights from April–September 1995 twice per month (N = 12 times) counting number of owls detected from spontaneous vocalizations without previous conspecific broadcasting (hereafter "calls"), and twice per month (N = 12 times) counting owls following broadcasts of tape-recorded owl vocalizations (hereafter "responses"). Travel time between survey stations ranged from 5–8 min. Surveys started during local twilight and continued for approximately 5.5 hr. Local twilight occurred from about 1830–1900 H during the period of the study.

To determine calls, we walked our survey trails and listened for owl calls for 10 min at each survey station, recording all individual owls that we heard or saw during this period (Anderson et al. 1985, Kochert 1986, Fuller

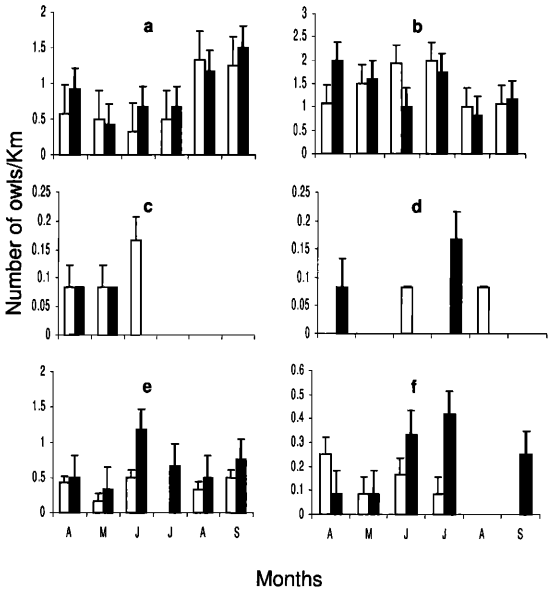

Figure 1. Average occurrence per km of trail/night, by month from April–September 1995, for (a) Vermiculated Screech-Owl, (b) Crested Owl, (c) Spectacled Owl, (d) Central American Pygmy-Owl, (e) Mottled Owl, and (f) Black-and-white Owl based on spontaneous calls (white bars) and responses to broadcasts (black bars) at La Selva Biological Station, Costa Rica. Error bar represents one standard error. Table 1 shows the total count of each species over 12 repetitions by each method over 3 2-km trails.

and Mosher 1987). To avoid counting the same individual, we estimated its location by compass triangulation (Bell 1964). While one of us triangulated an owl, the other person always remained at the survey station to record other individuals (same or different species) vocalizing within the 10-min period. We located individuals on a map of La Selva (scale 113 000).

Three days after counting calls, we used the same trail and survey stations to conduct a response count. Prior to our study, we recorded locally the characteristic vocalizations of Vermiculated Screech-Owl (*Otus vermiculatus*), Crested Owl (*Lophostrix cristata*), Spectacled Owl (*Pulsatrix perspicillata*), Mottled Owl (*Strix virgata*) and Black-and-white Owl (*S. nigrolineata*). We used a Uher 4000RL tape recorder and unidirectional Electro-Voice microphone to obtain vocalizations. We used a 3-min edited sequence of each species for playback and broadcast it with a Sony CFM-1605 cassette recorder. We divided each transect into two equal segments, then randomly selected the playback sequence of the five species and played the call of only one species at each station (Kochert 1986). Any one species' call was broadcast at only two stations along any one trail during any one night. A sampling period per station consisted of 3 min of broadcasting call followed by 7 min of silence and listening. During a single sampling period, we recorded responses of any owl to playback. We determined also the location of responding individuals by triangulation. Although the Central American Pygmy-Owl (*Glaucidium grisceiceps*) was not included in our original protocol, this species called spontaneously and responded to playback of interspecific calls during our study. Therefore, we included it in our results and analyses.

We recorded the following temporal and environmental conditions at each survey station: hour (number of hours after the official local sunset), days from solstice (the absolute number of days before or after the summer solstice, after Cooper 1981), moon phase (0 during period around new moon and 4 during period around full moon, with gradations in between, after Palmer 1987), illumination (from 0 for totally dark to 3 for as bright as night can be, after Palmer 1987), cloud cover (from 0 for no cloud to 3 for totally overcast, after Palmer 1987), and precipitation (0 for no rain to 3 for heavy rain). We also considered the mean temperature (maximum plus minimum divided by two) for the survey date at the Selva Biological Station.

Our sampling unit was any single trail surveyed any single night, and we expressed our owl occurrence index as the average number of individuals sighted or heard in a night per km of trail surveyed (Brower et al. 1990) The total occurrence value was the total number of individuals of any species detected with one of the two survey methods over the 6 mo of study (i.e., the total over the 12 repetitions by each method over 3 2-km trails) We reduced pseudo-replication by combining results for any one month.

We considered a species to be rare if the overall mean estimated occurrence was <0.1 individual per night/km of trail, uncommon if occurrence averaged between 0.1–0.85 owls per night/km of trail, and common if >0.85 owls per night/km of trail. We then calculated monthly averages for each species to evaluate changes in owl detectability throughout the study period. Fluctuations in monthly averages in spontaneous calls and responses were tested using Kolmogorov-Smirnov goodness-of-fit. For significant fluctuations, we determined significant categories using 95% Bonferroni confidence intervals (Neu et al. 1974). Occurrence distributions resulting from the two sampling methods were compared with Kolmogorov-Smirnov two-sample tests. To identify environmental variables that may have correlated with calls and responses, we used Spearman rank correlation analysis (Sokal and Rohlf 1981).

RESULTS

Vermiculated Screech-Owls and Crested Owls were common (Table 1). Mottled Owls and Black-and-white Owls were uncommon, while Spectacled Owls and Central American Pygmy-Owls were rare. Vermiculated Screech-, Crested, and Mottled Owls were recorded in all study periods (Fig. 1). Significant monthly variation in detections occurred for the Vermiculated Screech-Owl, Spectacled Owl, and Central American Pygmy-Owl (Table 2). Vermiculated Screech-Owls were detected less often

Table 2. Kolmogorov-Smirnov (D) goodness of fit values for fluctuations in mean monthly counts of six owls species using two survey methods from April–September 1995 at La Selva Biological Station, Costa Rica.

SPECIES	METHOD	MONTHLY MEAN (±SD)	D
Vermiculated Screech-Owl	Spontaneous calls	9.0 ± 5.1	0.317*
	Responses	10.7 ± 4.8	0.217
Crested Owl	Spontaneous calls	17.2 ± 5.3	0.279
	Responses	16.7 ± 5.2	0.182
Spectacled Owl	Spontaneous calls	0.7 ± 0.8	0.293
	Responses	0.3 ± 0.5	0.407**
Central American Pygmy-Owl	Spontaneous calls	0.3 ± 0.5	0.407**
	Responses	0.5 ± 0.8	0.390**
Mottled Owl	Spontaneous calls	3.8 ± 2.4	0.189
	Responses	7.8 ± 2.7	0.200
Black-and-white Owl	Spontaneous calls	1.2 ± 1.2	0.224
	Responses	2.3 ± 1.9	0.251

* $P \leq 0.05$.
** $P < 0.01$.

during June than in most other months. Spectacled Owls were detected only from April–June, while detections of the Central American Pygmy-Owl were scattered (Fig. 1, Table 2).

The broadcast survey method provided significantly more detections of Mottled Owls (Table 1). The two survey methods provided similar results for the Vermiculated Screech-Owl and the Crested Owl. Detections of other species were too few to meaningfully compare for the two methods.

Vermiculated Screech-Owls were positively associated with the number of days before or after the summer solstice (Tables 3, 4, Fig. 1). Generally other species were less detected away from the summer solstice (Fig. 1). For the spontaneous call technique the decrease away from the solstice was significant for Crested Owls and Spectacled Owls (Table 3), while with the response to broadcast technique the decrease away from solstice was significant only for Mottled Owls (Table 4).

For every species, the number of detections was negatively associated with the amount of illumination, though this relationship was statistically significant for only Mottled Owls (Table 3) and Crested Owls (Table 4). Detections were positively associated with moon phase, significantly so for Vermiculated Screech-Owls, Crested Owls and Mottled Owls (Table 3). The detection rate was high during dark periods when the moon phase was nearly full, either before the moon rose over the horizon or when clouds obscured the moonlight.

Detections were generally negatively associated with the number of hours since sunset, but this relationship was significant only for Spectacled Owls with the spontaneous call technique (Table 3).

Our results indicated that some of the owl species have increased in numbers at La Selva over the past 35 years (Table 5). In our study, Vermiculated Screech-Owls and Crested Owls were common, in contrast with previous records at La Selva.

DISCUSSION

The calling activity of some owls appears to be affected by moon cycles and light levels (Smith et al. 1987). At La Selva, moon phase and days from summer solstice affected vocal activity of some but not all of the owl species we encountered. Illumination had a negative effect with the calling activity of all owl species occurring more during dark nights and during dark periods of otherwise bright nights. This might seem to be contradictory with the positive association of vocalizations with moon phase but most of these responses occurred during dark moments around the full moon before the moon appeared in the horizon and increased illumination, or when clouds obscured the moon. By comparison, Northern Saw-whet Owls (*Aegolius acadicus*), Boreal Owls (*A. funereus*), and Western Screech-Owls (*Otus kennicottii*) have been reported to respond more during bright nights and full moon periods (Palmer 1987). Northern Spotted Owls (*Strix occidentalis*) responded more during quarter ebb (last quarter) and new moon (Ganey

Table 3. Correlation coefficients of spontaneous calls by five owl species with respect to temporal and environmental variables from April–September 1995 at La Selva Biological Station, Costa Rica.

	Species				
Variables (N)	V. Screech-Owl	Crested Owl	Spectacled Owl	Mottled Owl	Black-and-white Owl
Days from solstice (18)	0.463***	−0.294**	−0.064*	−0.064	−0.063
Hour (5)	−0.243	−0.163	−0.832*	−0.180	0.417
Illumination (4)	−0.947	−0.937	−0.698	−0.969*	−0.685
Cloud cover (4)	−0.066	−0.029	−0.083	0.191	−0.063
Moon phase (4)	0.617*	0.665**	0.216	0.571*	0.229
Temperature (8)	0.740	0.497	−0.353	0.677	0.178
Precipitation (4)	−0.214	−0.144	−0.258	−0.225	−0.008

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.

1990), whereas the response of Eastern Screech-Owls (*Otus asio*) to broadcasts has varied little across environmental conditions (Carpenter 1987, Smith 1987). The responsiveness of owls to broadcasts of conspecific calls apparently varies by species and geography.

Vermiculated Screech-Owls, Central American Pygmy-Owls, and Spectacled Owls exhibited significant variability of vocal activity among months. We were unable to correlate calling periods with breeding seasons, because little breeding information is available for most tropical owl species. Nonetheless, the differences that we observed in vocal activity of these species may have been associated with their breeding phenology. Indeed, understanding the year-long calling behavior of these owls is important for understanding their breeding phenology and to document population trends through repeated monitoring (Mathisen and Mathisen 1968).

For most species in our study, survey results did not differ between the two techniques. Mottled Owls were more frequently detected using call playback techniques than by using spontaneous calling. Gerhardt (1991) reported similar results in Guatemala. In North America, Eastern Screech-Owls and Elf Owls (*Micrathene whitneyi*) have also been recorded more frequently using playback techniques (Johnson et al. 1981). Broadcast vocalization has been an effective and useful method for counting temperate owls (McGarigal and Fraser 1985, Bosakowski et al. 1987, Zubergoitia and Campos 1998). In contrast, Great Horned Owls (*Bubo virginianus*) were detected more often from spontaneous calls than from responds to broadcasts (Springer 1978). Intra- and interspecific competition could play a major role in response patterns while using the playback method (Enríquez and Rangel-Salazar 1997).

Slud (1960) mentioned only one record for the Vermiculated Screech-Owl and recorded the Crested Owl as rare at La Selva Biological Station. Subsequently, Janzen (1991) reported Crested Owls as occasional and Vermiculated Screech-Owls as uncommon. Spectacled Owls and Central American Pygmy-Owls were previously reported as common by Slud (1960) and later as uncommon (Janzen 1991, Levey and Stiles 1994). During our study, we recorded so few individuals of both species that we classified them as rare. Mottled Owls were abundant or common, but we found them to be uncommon. Barn Owls (*Tyto alba*) occur at La Selva but

Table 4. Correlation coefficients of responses by four owl species to broadcasts of calls with respect to temporal and environmental variables from April–September 1995 at La Selva Biological Station, Costa Rica.

	Species			
Variables (*N*)	V. Screech-Owl	Crested Owl	Mottled Owl	Black-and-white Owl
Days from solstice (18)	0.325*	0.209	−0.402**	−0.049
Hour (5)	−0.112	−0.133	−0.923	0.137
Illumination (4)	−0.854	−0.984*	−0.841	−0.822
Cloud cover (4)	−0.023	0.241	−0.315	−0.513
Moon phase (4)	0.283	0.413	0.353	0.389
Temperature (8)	0.198	0.487	0.345	0.169
Precipitation (4)	−0.136	−0.253	−0.294	−0.302

* $P < 0.05$.
** $P < 0.01$.

were not recorded near our survey trails; therefore, we did not estimate any occurrence for this species. We did not record Andean Pygmy-Owls (*Glaucidium jardinii*) or Striped Owl (*Asio clamator*), though both species have occasionally been recorded at La Selva during Christmas Bird Counts (CBC 1985–94). Previous owl records at La Selva were part of attempts to ascertain occurrence of all avifauna without specifically targeting owls, so our study should have detected owls at a higher rate than previous studies.

The Crested Owl has been reported to be associated with mature forest and mature second-growth forests for nesting and roosting (Marcot 1995). However, it apparently tolerates limited deforestation (Hume 1991, König et al. 1999). Crested Owls have apparently increased in abundance at La Selva, whether because of breeding success or immigration of individuals displaced by cutting of surrounding forests.

The Spectacled Owl is associated with dense forest with old trees, and may also occur in forest edges and plantations (König et al. 1999). It was recorded as common by Slud (1960) and rare in our study. Although it tolerates more deforestation than the Crested Owl (Hume 1991), our results suggest that it has apparently decreased at La Selva.

The Mottled Owl has been reported to be the most abundant owl in Neotropical rainforests and has a wide distribution range (Gerhardt et al.

Table 5. Owl species abundance (A = Abundant, C = Common, U = Uncommon, R = Rare, O = Occasional, O^2 = only one record, — = no report) over three decades at La Selva Biological Station, Costa Rica.

	Studies[1]					
Species	S (1960)	T (1990)	J (1991)	L and S (1994)	CBC (1985–94)	E and R (1995)
Barn Owl	—	U	U	U	U	O^2
Vermiculated Screech-Owl	O^2	U	U	U	UC	C
Crested Owl	R	O	O	UC	UC	C
Spectacled Owl	C	U	U	U	U	R
Central American Pygmy-Owl	C	U	U	U	U	R
Andean Pygmy-Owl	—	—	—	—	O	—
Mottled Owl	A	C	C	UC	UC	U
Black-and-white Owl	—	R	R	R	R	U
Striped Owl	—	—	—	—	O	—

[1] S = Slud (1960), T = Taylor (unpublished data), J = Janzen (1991), L and S = Levey and Stiles (1994), CBC = Christmas Bird Counts, La Selva (1985–94), E and R = (1995), this study.

1994). Mottled Owls are considered tolerant to some deforestation, and can be found near forest edges, semi-open areas, and secondary mature forests (Stiles and Skutch 1989). Nonetheless, Mottled Owl populations may have decreased at La Selva during the past 30 years. The Black-and-white Owl was also uncommon during our study. Unlike the Mottled Owl, it is considered to be rare throughout its range and has been classified as uncommon in Costa Rica (Stiles and Skutch 1989). Black-and-white Owls are associated with dense and mature forests (Marcot 1995), and La Selva might act as a refuge for it.

Our results suggest that owl occurrence has been changing at La Selva. Levey and Stiles (1994) predicted changes in populations of birds, and habitat loss has been identified as the principal factor affecting populations of tropical raptors (Thiollay 1994). In the Neotropics, protected areas such as reserves and national parks often function as refuges for many species of wildlife that depend on forested habitats (Terborgh et al. 1990). Spectacled Owls and Mottled Owls have been thought to tolerate forest fragmentation (Hume 1991), but they appear to have decreased in occurrence at La Selva. Further studies of the ecology of tropical owls would be useful in identifying the life history components most affected by human disturbance.

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