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# Bird Behaviour during Prey-Predator Interaction in a Tropical Forest in México

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## Abstract

Birds emit alarm calls, considered as honest signals, because they communicate the presence of a predator or potential threat. We evaluated behavioural events of birds responding to vocal and visual stimuli of a nocturnal predator (black-and-white owl *Ciccaba nigrolineata*) and a diurnal predator (collared forest falcon *Micrastur semitorquatus*). We analysed variations in behavioural events seasonally (reproductive and nonbreeding) and by bird size, as well as their relationship with the vegetation structure and landscape. The study was performed during the breeding (March-May) and non-breeding seasons (February, June and July) of 2016 in Chiapas, Mexico. We used four transects with different vegetation types and land uses. The most frequent behavioural response by birds to the vocal stimuli of the black-and-white owl and the collared forest-falcons was vocal, during the breeding season, and small species responded the most to the stimuli (p = 0.008) and (p < 0.015), respectively. We identified two vegetation and two landscape variables associated in 36% of probability for the prey to respond to black-and-white owl vocal stimuli, three variables of vegetation and one of the landscape in 37% for the collared forest-falcon stimuli. Potential prey animals modify the behaviour, which allows them to detect, evade or confront a predator.

**Keywords:** signs, *Ciccaba nigrolineata*, *Micrastur semitorquatus*, stimuli, mobbing, environmental variables

## 1. Introduction

Ecological interactions are the basic components that structure and stabilise the biological diversity of ecosystems and are important for communication among individuals [1, 2]. Communication involves the transmission of information (signals) from one individual to another [3]. Signals are the exchange of information from a sender (individuals) that provokes the response of a receiver; they may be conspecific or hetero-specific [3–5]. There are three types of signals between individuals: visual, vocal and olfactory. In the case of prey-predator interaction, visual recognition of a predator relies on previous experience, while vocal recognition involves learning to detect the presence of predators [5, 6].

Birds make alarm calls that are honest signals (i.e. it implies a benefit to the sender and/or receiver), and these signals are used to alert the presence of a potential predator or threat [3, 7, 8]. Predators limit the abundance of their prey populations [9, 10]. However, prey availability may be a factor regulating the abundance of predators [11]. Mobbing (i.e. aggregations or harassment [12, 13]) is considered a behaviour in birds to deal with predators; it is carried out by bird species at a risk of predation or other potential threats, which are identified visually or vocally [14, 15]. Mobbing is considered an anti-predator adaptation for survival and reproduction [16, 17]. In some bird species, the intensity of mobbing varies temporarily. For example, the mobbing behaviour of the European pied flycatcher (*Ficedula hypoleuca*), the American robin (*Turdus migratorius*) and the house finch (*Haemorhous mexicanus*) is more intense during the breeding season because they defend their territory and share parental care [13, 18–20]. Also, the costs and benefits of being a participant in mobbing vary according to the size of the bird. Small species can unite to avoid being attacked since they are often more easily depredated alone [15, 21]. On the contrary, birds of greater size are more difficult to depredate [15, 22].

Response behaviours (e.g. attacking, fleeing and vocalising) of prey are influenced by environmental factors and previous experience of the organism [23]. Most species exhibit aggressive-defensive behaviours such as threatening gestures, body postures (different body positions of head or wings) and attacks or may show submission behaviours such as escaping or standing still [23]. One way to evaluate the different response behaviours of birds is through the playing of pre-recorded vocalisations and by providing visual stimuli of their potential predators [24]. The use of vocal and visual stimuli of the predators allows for evaluating the response behaviour of the potential prey [13, 24].

Prey responds to the risk of depredation by altering its behaviour (e.g. changes in vigilance or in the search for food) or by avoiding high-risk areas [25]. These changes in behaviour allow prey to escape approximately 80% of the time from attempts to be caught by predators [26]. Therefore, prey can learn and thereby respond to distinct levels of risk and fear of predation [27, 28]. According to the 'ecology of fear' theory, the prey will avoid areas of predator abundance to reduce the probability of being depredated or will use suitable sites to rapidly escape [28]. It is important to study the prey-predator relationships to completely understand such interactions. In this context, the objectives of this study were to analyse the bird behaviours that respond to vocal and visual stimuli of a nocturnal raptor, the black-and-white owl, and a diurnal, the collared forest falcon between seasons, bird sizes and their relation to the vegetation structure and landscape.

## 2. Materials and methods

### 2.1 Study area

The study was carried out in the La Selva El Ocote Biosphere Reserve (REBISO), located in the northwestern portion of the state of Chiapas (between 16° 45′ 42″ and 17° 09′ 00″ North; 93° 54′ 19″ and 93° 21′ 20″ West; **Figure 1**). The reserve covers an area of 101,288 ha, with elevations ranging from 200 to 1450 m a.s.l. [29]. Emilio Rabasa Ejido is located in the buffer zone and characterised by a semi-deciduous forest landscape, secondary vegetation and different land uses such as pasture, agricultural fields and human settlements [29]. The sampling points covered diverse types of vegetation and land use.
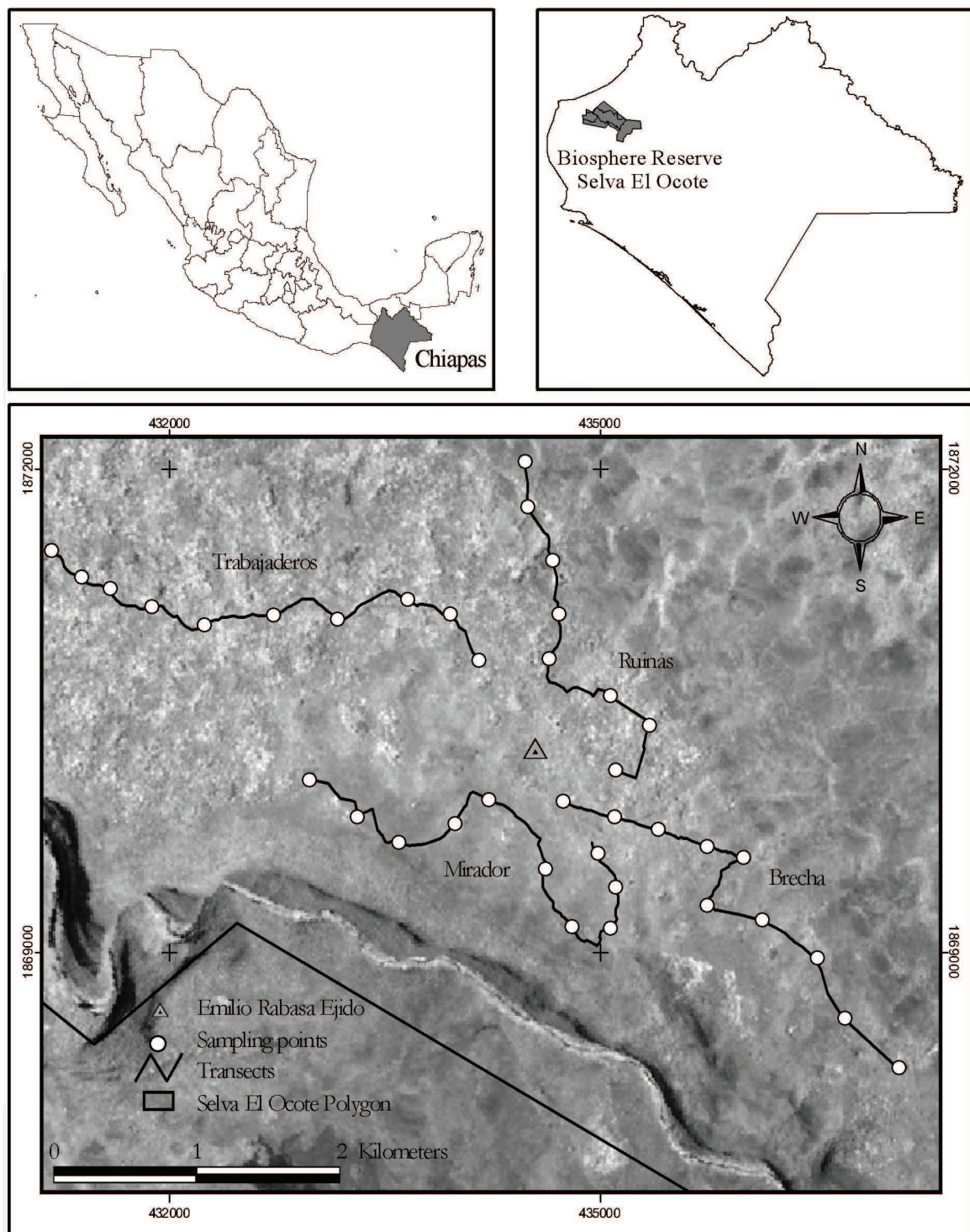
**Figure 1.**
*Geographic location of four transects and sampled points in La Selva El Ocote Biosphere Reserve, Chiapas, Mexico.*

## 2.2 Predatory species used as a model

Nine nocturnal species of raptors have been recorded in the La Selva El Ocote Biosphere Reserve [30]. Three of them (black-and-white owl, *Ciccaba nigrolineata*; ferruginous pygmy owl, *Glaucidium brasilianum*; and spectacled owl, *Pulsatrix perspicillata*) include birds in their diet [31–33]. Twenty-five diurnal raptors have also been recorded [30], of which the collared forest falcon and the barred forest falcon (*M. ruficollis*) feed mainly on birds [33, 34]. The predators used as a model in this study were selected based on their dietary habits (mainly birds) and hunting

behaviour in the interior of the forest [34]. We selected the black-and-white owl and the collared forest falcon as the best that met these criteria.

## 2.3 Description of the predators

The black-and-white owl is a medium-sized owl (average 39 cm) with a wide distribution in the Neotropical region and apparently stable populations [35]. However, its populations may be locally declining because of habitat transformation or fragmentation. This species feeds on small birds such as thrushes (*Turdus* sp.), burnished-buff tanager (*Tangara cayana*), blue-grey tanager (*Thraupis episcopus*) and silver-beaked tanager (*Ramphocelus carbo*) [31, 36].

The collared forest falcon is a medium-size forest hawk (average 55 cm) which feeds on birds and small mammals [34]. Species of birds reported as its prey include the crested guan (*Penelope purpurascens*), the great curassow (*Crax rubra*), the plain chachalaca (*Ortalis vetula*), the spotted wood quail (*Odontophorus guttatus*), the keel-billed toucan (*Ramphastos sulfuratus*), the golden-fronted woodpecker (*Melanerpes aurifrons*) and the brown jay (*Cyanocorax morio*) [34, 37].

## 2.4 Field methods

In previous surveys during February and August 2015, the *ad libitum* recording method was used, which consists of opportunistic observations of behavioural events, without restrictions on time and observations (of bird species), on a continuous basis [38, 39]. With this method, behavioural events (short-term behavioural patterns that can be expressed as frequencies [38]) of some birds were recorded during the emission of vocal stimuli of the black-and-white owl and the collared forest falcon calls. Based on these observations and with references from the literature [22, 40, 41], we obtained an ethogram of the description of species' behaviour [38] (**Table 1**). With this ethogram, the birds' behaviour was classified into nine categories, which were used as a basis for determining the behaviour

| Behavior category | Behavior | Detection type | Description |
|---|---|---|---|
| Silent answer | still | Visual | Individual is without any movement, standing or in rest position |
| Silent response with movement | vigilance, without vocalizing | Visual | It moves from one place to another, using the legs (soil, branches) and observes its surroundings turning head and body |
| Silent response with movement | escape | Visual | Individual moves away from the site and does not return |
| Response with movement | escape - vocalizing | Visual, vocal | Individual moves away from the site vocalizing |
| Low intensity mobbing | vigilance-vocalizing | Visual, vocal | It moves from one place to another, using the legs (soil, branches)vocalizing |
| Low intensity mobbing | vocalize (alarm call) | Vocal | Vocalization can be loud and repetitive or sporadic and performed when there is a danger signal (they are shown) |
| Low intensity mobbing | stay-vocalizing | Vocal | Individual (s) is on a site and vocalizing |
| High intensity mobbing | approach-vocalizing | Visual, vocal | Vocalizations and movements are constant (they look for the predator), but they do not detect it visually to attack it |
| High intensity mobbing | attack | Visual, vocal | Direct attack, vocal / visual stimulus was detected and attacked. |

**Table 1.**
*Ethogram of potential prey, in response to vocal and visual stimuli of black-and-white owl and collared forest falcon.*

during the samplings. Low-intensity mobbing was considered by prey birds when the behaviour of one or more individuals/species changed, mostly due to a vocal response (except for some records where the birds were observing and/or vocalising but remained in the place). On the other hand, high-intensity mobbing was considered from two or more individuals/species and when the recording involved visual, vocal, search, approach and attack behaviours.

## 2.5 Sampling design

An independent paired experimental design was used to measure the responses before and after applying a single treatment (vocal and visual stimulus), using the organism as its own control. The study was of transversal type, in which we compared the behaviour of different individuals in a determined period [38, 39]. To register the responses of the birds to the predator stimuli, we established four transects [42]. Three transects were 4 km long and one was 3.2 km. Sampling points were established on every route, 400 m apart from each other ($n = 38$). To determine temporal variations (monthly and between the breeding and non-breeding seasons) in the response of potential prey, the sampling period comprised 6 months. In this study, March, April and May were considered as the reproductive season, and June, July and February as the non-reproductive season. We created three categories of bird size: small (10–17 cm), medium (18–21 cm) and large (22–55 cm) [43–45]. All bird species were considered in the analyses, even migratory species. These species are exposed to predators that take advantage of the depletion of these birds [46].

Vegetation and landscape variables were measured in each sampling point and related to behavioural events [47, 48]. The vegetation variables measured were: (a) number of logs, (b) number of live trees, (c) percentage of canopy cover, (d) height of vegetation strata (undergrowth, medium and canopy) and (e) disturbance level of vegetation (with a scale of: 0 = absent, 1 = low, 2 = median and 3 = high). The landscape variables were: (a) distance to roads, (b) distance to dwellings, (c) presence-absence of water sources, (d) presence-absence of open areas (agricultural area, coffee plantation and pastures), (e) land topography (top, valley and slope) and (f) slope in degrees [49].

## 2.6 Sampling

All behaviours were recorded using focal sampling (i.e. observations of an individual or a group during a determined time). The observations consisted of 9 min at the point of sampling, which allows the detection of several behaviour categories [38, 50]. In addition, we recorded birds performing all behaviours at the time of sampling [39, 50]. Sampling was done in the morning (05:00 to 09:00 h) and evening hours (15:30 to 19:30 h). Each sampling session was 9 minutes, starting with the first 3 minutes in silence to record the presence of any bird species, followed by 3 minutes with an emitted vocalisation of a predator and 3 minutes in silence to record any response [51]. Behavioural events of the birds were recorded during the playing of the vocal stimulus and during the last 3 minutes. The loudspeaker (Radio Shack Power Horn model) used was carried by a second observer, who directed it towards the four cardinal points. In each point, we used visual stimuli [13, 24], which were a plastic owl (morphologically similar to a black-and-white owl) and two-actual size colour photographs of the collared forest-falcon stuck together to have a double view. The plastic owl and the printed image were placed at each sampling point at a height of 6 m above the ground, supported by two tubes with extension.

Pre-recorded vocalisations of the black-and-white owl (at four sampling points) were played during the first 2 h of the morning (05:00 to 07:00) sampling, and at a random point, a different vocalisation (spectacled owl) was played. This was done to avoid habituation of the species to the vocal stimulus [8]. After 2 hours of sampling, the vocalisation of the collared forest-falcon was broadcast, and at one point, the vocalisation of its conspecific, the barred forest-falcon, was issued randomly. The evening sampling began with the broadcast of the collared forest-falcon vocalisation (first 2 hours) and finished with the black-and-white owl vocalisation.

Vocalisations used as stimulus were obtained from Fonoteca de las Aves de Chiapas [52] and xeno-canto (http://www.xeno-canto.org/). We used common vocalisations from three different individuals of each of the black-and-white owl, the spectacled owl, and the collared and barred forest-falcons, 3 minutes cut with ADOBE AUDITION CS5.5. ® [53], to avoid pseudo-repetitions [54, 55]. In each sampling point, we recorded the songs or calls of bird species that answered to the stimulus. Recordings were made with a SONY recorder model PCM-M10 with a SONY microphone model ECM-MS907 to identify the bird songs. In addition, a CANON camera model SX530 HS was used to photograph and record the birds' behaviour during or after the stimuli.

## 2.7 Statistical analysis

Generalized linear mixed models (GLMMs) were used to analyse the frequency variation of the behaviour events, breeding and non-breeding seasons and bird sizes. Behavioural types, months, seasons and bird size were considered as fixed effects, while transects and seasons were considered random effects. For the analysis of similarity between months and breeding and non-breeding seasons, we used the Bray-Curtis index, where 1 means 100% similar and 0 means that there is no similarity [56]. For this analysis, we used the EstimatesS version 9 and InfoStat/E version 2007 program, with a link to the program R 3.3.2 [57, 58].

To determine the relationship between vegetation structural variables and landscape variables with response behaviours of potential prey, we used the binary logistic regression model. The response behaviours were the binary-dependent variables, while vegetation and landscape variables were independent variables. The variables were selected using a combined method of backward elimination and forward selection to obtain the best fit model. We used the coefficient of determination ($r^2$) to explain the responses of the species in certain sites. The results of the likelihood ratio test were used to explain the weight of each of the variables in the model. This analysis was performed with the JMP-SAS 7.0 program [59]. All statistical analyses were considered significant at $p \leq 0.05$.

## 3. Results

### 3.1 Species that responded to stimuli

A total of 596 vocal stimuli of the black-and-white owl and 512 of the collared forest falcon were performed across a total of 528.4 km. We recorded 68 bird species of 12 orders and 28 families, with a total of $n = 574$ response behaviours (Appendix 1). Families with the highest number of responses were Ramphastidae 14% (n = 81), Corvidae 13% (n = 74) and Tyrannidae 9.5% (n = 55). Other families recorded were Tinamidae, Accipitridae and Thamnophilidae. Thirty-eight species (56%) responded to both predators, but at different frequencies. For example, the

long-tailed manakin (*Chiroxiphia linearis*) responded six times to the black-and-white owl and 18 times to the collared forest-falcon. The white-breasted wood wren (*Henicorhina leucosticta*) responded 17 times to the black-and-white owl and seven times to calls from the collared forest-falcon. From the yellow-throated euphonia (*Euphonia hirundinacea*), the fan-tailed warbler (*Basileuterus lachrymosus*), the red-billed pigeon (*Patagioenas flavirostris*) and the pale-billed woodpecker (*Campephilus guatemalensis*), a single response was obtained to both predators (Appendix 1).

For the black-and-white owl stimuli, 51 bird species belonging to 10 orders and 25 families responded. Four of these species were migratory (olive-sided flycatcher (*Contopus cooperi*), Swainson's thrush (*Catharus ustulatus*), magnolia warbler (*Setophaga magnolia*) and summer tanager (*Piranga rubra*). The species with the highest number of behavioural events was the keel-billed toucan with 13.5% (n = 37), followed by the white-breasted wood wren with 6% (n = 17) and the mottled owl (*Ciccaba virgata*), collared forest-falcon and gartered trogon (*Trogon caligatus*), with 5% (*n* = 14) each. Thirteen bird species were recorded only once (e.g. yellow-billed cacique, *Amblycercus holosericeus*; fan-tailed warbler; black-faced grosbeak, *Caryothraustes poliogaster*; and yellow-throated euphonia).

The bird responses to the stimuli were individual or of two, three and up to four individuals of the same or different species. The white-breasted wood wren was the species with the highest number of individual behavioural events (*n* = 17), followed by the bright-rumped attila (*Attila spadiceus*) and the blue-diademed motmot (*Momotus lessonii*) (*n* = 11). There were 179 events of individual behaviour (from stay still until to attack); most of the birds only vocalised (129), 16 escaped, 12 vocalised and stayed in one place, 7 stay still (e.g. olive-sided flycatcher, red-throated ant-tanager (*Habia fuscicauda*) and white-breasted wood wren), 7 escaped and vocalised, 5 approached with vocalisations and 3 attacked (i.e. collared forest-falcon, royal flycatcher (*Onychorhynchus coronatus*) and green shrike-vireo (*Vireolanius pulchellus*).

We obtained 70 response behaviour events with groups of two individuals, of which in 50 events, the birds only vocalised, 10 escaped (e.g. long-tailed manakin, boat-billed flycatcher, *Megarynchus pitangua* and brown jay), 4 stayed in one place while vocalising, 2 escaped while vocalising, 2 approached while vocalising and 2 attacked (e.g. yellow-green vireo, *Vireo flavoviridis*). The species which showed more responses with two individuals was the keel-billed toucan with the highest number of behavioural events (*n* = 20), followed by the brown jay (*Psilorhinus morio*) and the black-and-white owl as an intraspecific response (n = 8). We recorded 18 behavioural events with 3 individuals; 6 escaped (3 from red-legged honeycreeper, *Cyanerpes cyaneus* and 3 from green jay, *Cyanocorax yncas*) and 12 vocalised with 3 events each; red-legged honeycreeper, brown jay, keel-billed tou-can and masked tityra, *Tityra semifasciata*. We recorded 12 events of behaviour with four individuals; all of them were from the keel-billed toucan; 4 escaped while vocalising, 4 only vocalised and 4 stayed and then vocalised.

There were 12 events recorded of high-intensity mobbing towards black-and-white owls. The bird species were the mottled owl, keel-billed toucan, collared forest-falcon, boat-billed flycatcher, bright-rumped attila, royal flycatcher, yellow-green vireo and green shrike-vireo. We identified seven different behaviours of potential prey of black-and-white owl. Vocalisation was the most frequent behavioural response ($\chi^2_{6,32} = 53.68$, $p < 0.001$; **Figure 2**).

Fifty-five bird species of 11 orders and 27 families responded to collared forest-falcon stimuli. Three of these species were migratory (yellow-green vireo, Swainson's thrush and summer tanager). The keel-billed toucan was the species that had more behaviour events with 14.5% (*n* = 42), followed by the collared forest
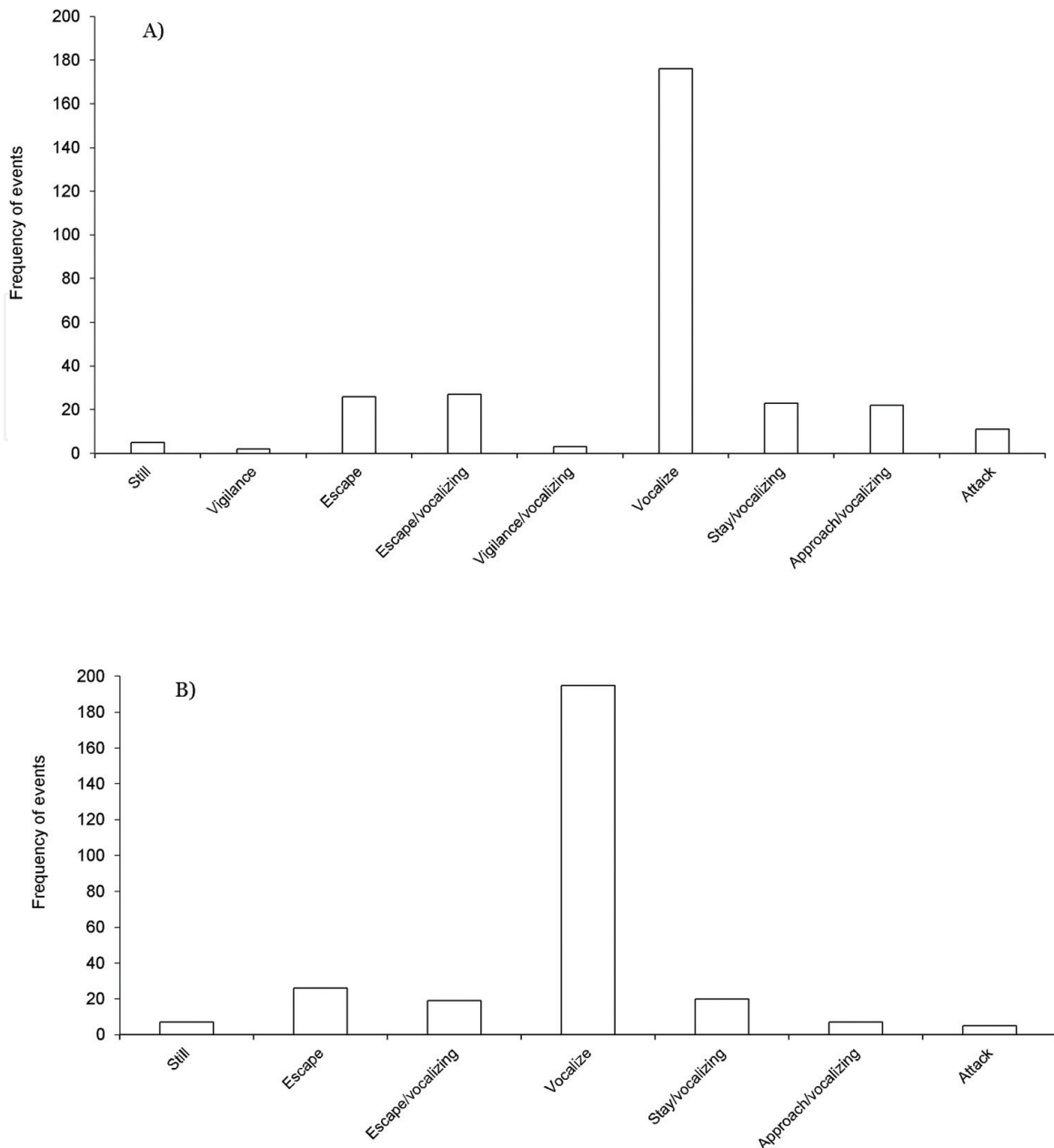
**Figure 2.**
*Frequency of events for each behaviour recorded from potential prey after vocal and visual stimuli of (A) black-and-white owl and (B) collared forest falcon in La Selva El Ocote, Chiapas, during February-July in 2016.*

falcon with 9% (*n* = 26), the brown jay with 7.5% (*n* = 22) and the long-tailed manakin with 6% (*n* = 18). Twenty species had only one behavioural event (e.g. fan-tailed warbler, pale-billed woodpecker and ruddy woodcreeper (*Dendrocincla homochroa*), bronzed cowbird (*Molothrus aeneus*) and red-billed pigeon).

The highest number of individual behaviour responses within a species to the collared forest falcon stimuli was interspecific (*n* = 20), followed by the gartered trogon (9), the keel-billed toucan (8), the long-tailed manakin (7) and the social flycatcher, *Myiozetetes similis* (7). We recorded 150 events of one individual response, most of them vocalised (107), 13 escaped, 8 approached vocalising, 6 escaped and vocalised, 6 vocalised and stayed, 5 stay still, e.g. bronzed cowbird, northern bentbill *Oncostoma cinereigulare* and citreoline trogon *Trogon citreolus*), and 3 attacked (i.e. red-throated ant-tanager and social flycatcher). The species that responded in groups of two individuals and had more behaviour events were the keel-billed toucan (*n* = 16) and the green jay (*n* = 10), with interspecific responses (collared forest-falcon; *n* = 8). Sixty-eight events were from 2 individuals, 46

vocalised, 8 approached and vocalised, 6 escaped and vocalised, 4 stayed and vocalised, 2 escaped and 2 attacked (i.e. collared forest-falcon).

From groups of three individuals that responded to the collared forest falcon stimuli, we recorded 54 events, of which 15 vocalised, 15 escaped and vocalised, 9 stayed and vocalised, 6 escaped (e.g. white-tipped dove, *Leptotila verreauxi* and brown jay), 6 approached and vocalised (i.e. white-throated magpie-jay, *Calocitta formosa*) and 3 were vigil and vocalised. The brown jay had the highest response events (12), followed by the white-throated magpie-jay (9) and the keel-billed toucan (9). Three behaviour events were recorded with groups of four individuals; red-legged honeycreeper, plain chachalaca and keel-billed toucan. In this study, we observed only one event of escape from a group of five keel-billed toucans responding to the stimuli of the collared forest-falcon and one of attack from six white-throated magpie-jays. In addition, we recorded 33 high-intensity mobbing events. The species recorded with mobbing were the white-throated magpie-jay, the brown jay, the boat-billed flycatcher and the gartered trogon. Finally, for the collared forest-falcon, we identified nine behavioural responses, with vocalisation being the most frequent one ($\chi^2_{8,36}$ = 35.07, $p < 0.001$; **Figure 2**).

## 3.2 Similarity of potential prey regarding the frequency of response behaviours and months

Similarity analysis showed that potential preys that responded to black-and-white owl stimuli were 57% similar in March and April (**Figure 3**). In these months, the highest number of behaviour events was observed ($\chi^2_{5,24}$ = 10.29, $p < 0.001$). However, the highest number of species that responded to black-and-white owl stimuli was observed in April and May ($\chi^2_{5,24}$ = 5.72, $p < 0.002$). For the collared forest-falcon, also in March and April, we observed a higher similarity of potential preys with 45%, while in April and June, the similarity was 41% (**Figure 3**). April showed the highest species richness and February the lowest ($\chi^2_{5,24}$ = 7.09, $p < 0.008$). The highest frequency of behavioural events was observed in April ($\chi^2_{5,.24}$ = 12.06, $p < 0.001$).

## 3.3 Frequency of response behaviours of potential preys during reproductive and non-reproductive seasons

Sixty-eight potential prey species responded to black-and-white owl stimuli during the entire study, of which 28 were recorded in both seasons (breeding and
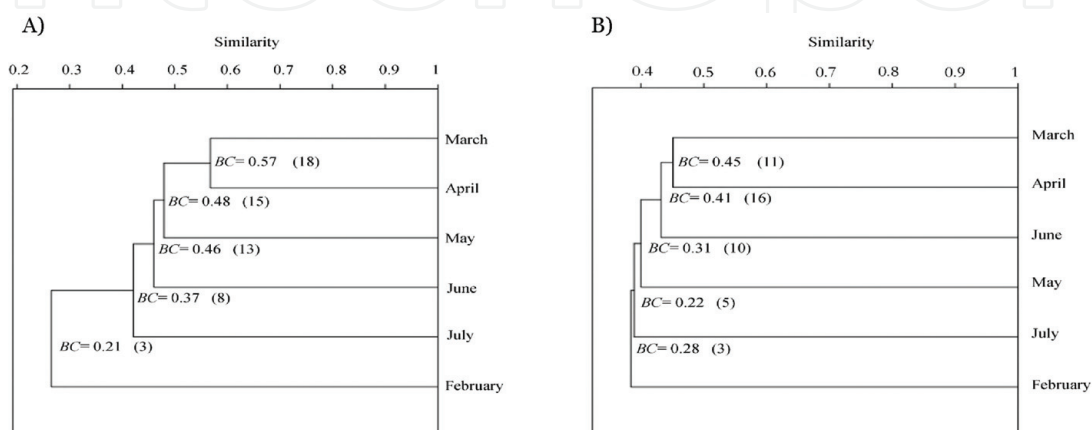


**Figure 3.**
*Similarity of potential prey that answered to the vocal and visual stimuli of (A) black-and-white owl and (B) collared forest falcon between months of 2016, in La Selva El Ocote, Chiapas.*

nonbreeding), with a similarity of 49%. During the breeding season, we observed the highest species richness and the highest number of behaviour events ($\chi^2_{1, 6} = 8.78$, $p < 0.041$; $\chi^2_{1, 6} = 7.34$, $p = 0.05$). For the collared forest-falcon stimuli, 68 potential prey species responded, and 24 were recorded in both seasons ($BC = 0.508$). Species richness was not different between seasons ($\chi^2_{1,6} = 3.52$, $p \geq 0.134$), but there were more behaviour events during the breeding season ($\chi^2_{1,6} = 7.24$, $p = 0.05$).

## 3.4 Frequency of behaviour events in relation to the size of potential preys

We observed variations in the size of potential preys according to the response behaviours obtained from the vocal and visual stimuli of the black-and-white owl ($\chi^2_{2, 12} = 8.29$, $p = 0.008$). Small species (e.g. social flycatcher, summer tanager, red-crowned ant-tanager *Habia rubica*, bright-rumped attila and masked tityra) showed a higher number of responses than larger species (e.g. pale-billed wood-pecker, pheasant cuckoo *Dromococcyx phasianellus*, collared aracari *Pteroglossus torquatus*). For collared forest-falcon stimuli, the number of behaviour events was also different between bird sizes ($\chi^2_{2, 12} = 6.91$, $p \leq 0.015$); it was greater in small species (e.g. royal flycatcher, social flycatcher, boat-billed flycatcher) than in larger ones.

## 3.5 Vegetation and landscape variables associated with behaviour events

The occurrence of behaviour events in response to black-and-white owl stimuli was associated with the habitat variables canopy height and number of live trees; at the landscape level, the presence or absence of an open area and the presence or absence of a water source were important factors. These four variables were associated in 36% of probability that potential prey could respond to the vocal and visual stimuli of the black-and-white owl ($r^2 = 0.36$, $X^2 = 15.20$, $p < 0.004$). For example,

| Species | Variables | Estimate | Effect of likelihood ratio |
|---|---|---|---|
| Black-and-white Owl *Ciccaba nigrolineata* ($r^2$=0.36, $X^2$=15.20, $p$<0.004) | Open area | 5.89 | $X^2$=11.61, $p$<0.0007 |
| | Canopy height (m) | 0.27 | $X^2$=5.26, $p$<0.0218 |
| | Presence or absence of a water source | -12.33 | $X^2$=3.14, $p$<0.0762 |
| | Number of live trees | -0.29 | $X^2$=1.75, $p$<0.1857 |
| Collared- forest Falcon *Micrastur semitorquatus* ($r^2$=0.37, $X^2$=12.40, $p$<0.014) | Canopy height (m) | -0.35 | $X^2$=5.43, $p$<0.0197 |
| | Presence or absence of secondary vegetation | 3.24 | $X^2$=3.99, $p$<0.0457 |
| | Number of live trees | 0.42 | $X^2$=2.92, $p$<0.0873 |
| | Number of dead trees | 0.95 | $X^2$=3.04, $p$<0.0808 |

**Table 2.**
*Vegetation and landscape variables that influenced a higher probability of recording response behaviours of birds as potential prey for black-and-white owl and collared forest falcon.*

our results indicate that in an open area with surrounding vegetation with a canopy higher than 14 m, species will be more likely to respond to the stimuli, and they will also be more likely to respond if there is a lower probability of finding a source of water or live trees with an understory less than 14 m in height (**Table 2**). Four vegetation variables explained a high response event to collared forest falcon stimuli ($r^2 = 0.37$, $X^2 = 12.40$, $p < 0.014$). The variables were secondary vegetation, number of dead trees (stumps and fallen logs), number of live trees (>1 m in diameter) and lower canopy height (<12 m).

## 4. Discussion

### 4.1 Response behaviour

In this study, vocalising (predation risk signal) was the highest response of potential prey to both predators. Vocalisation involves energy costs and exposure to predators [60], which vary according to the duration, intensity and acoustic frequency. However, some bird species have developed the ability to transmit vocal signals more frequently to alert members of the flock about the presence of a potential threat [61]. Bird species responded more frequently to vocal stimuli than to visual ones. For example, a bird species' visual detection of a collared forest falcon could be more difficult because it lives inside the forest and is morphologically adapted to hunt inside and at the edges of the forest [33, 62]. Vocal signals or alarm calls can be an adaptation of the prey birds to communicate to other species that an avian predator is nearby.

Species that responded most frequently to vocal stimuli belonged to the families Ramphastidae, Corvidae and Tyrannidae. These species may face potential threats from predators due to their life history traits such as eating habits (feeding in the canopy or the interior of the forest). Species of the families Corvidae (green jay, brown jay and white-throated magpie-jay) and Tyrannidae (boat-billed flycatcher and dusky-capped flycatcher, *Myiarchus tuberculifer*) perform most of their activities in groups, which could make them more evident by increasing encounters with predators [43]. Members of the Tyrannidae family perform behaviours such as watching and escaping to avoid being captured by a predator. We recorded attack behaviour of the royal flycatcher and the social flycatcher and escape behaviour of the boat-billed flycatcher and the bright-rumped attila. Observations of predator species' food habits and optimal foraging show that more abundant prey species are depredated at a higher rate, because the predator minimises foraging time and maximises the energy efficiency [63].

Detecting and emitting signals involve costs (the probability of being found and attacked by a predator) and benefits (increasing survival for the rest of the group) [64, 65]. However, if fewer birds are watching during foraging, this could increase the risk of predation [66]. In this study, bird species as potential prey used vocalisations to help other individuals (in this case escape from the site) or to transmit to the predator that it is willing to combat, even if the cost of this action is death.

We obtained 45 responses of escape to the black-and-white owl stimuli and 53 to the collared forest-falcon stimuli. This type of response has also been observed in the Eurasian blue tit (*Cyanistes caeruleus*) and the great tit (*Parus major*) to a potential threat, consisting of moving between the trees or flying towards the

canopy. If the predator is on the ground, vertical movement may be the safest escape option [67]. In this study, the escape of potential prey consisted of detecting the bird visually, and after the vocal stimuli, the individuals looked around, some moved to a tree, extended their wings and entered into a monitoring mode (moving the head from side to side); they finally escaped among the trees.

The plain chachalaca and the spotted wood quail have been reported to escape into the vegetation and vocalise, but they can also use the attacking behaviour by flying near the vegetation to chase the predator [22]. From our observations in the field, chachalacas, which are noisy by nature, with two or more individuals in one site, respond to any sound that implies a threat by increasing their vocalisations. For pigeons (white-tipped dove, red-billed pigeon and white-winged dove, *Zenaida asiatica*), we identified events of individuals escaping, events of vocalisation, and events where one individual approached and vocalised. Pigeons associated with open areas (i.e. white-winged dove) apparently escape individually or socially by flying fast. However, they may also seek shelter when they are alone and/or under pressure from a predator [22]. Pigeons performed the escape behaviour with individual movements among the vegetation; only the white-winged dove, instead of escaping, approached the visual stimulus and began to vocalise when it was near. Vocalisations indicate that pigeons gave notice to their conspecifics of the presence of the predator, without moving from their shelter.

Woodpeckers responded by moving to the opposite side of the trunk and then escaped the site [22]. We obtained two behaviour events for the pale-billed woodpecker: one escaped and the other only vocalised; in contrast, the lineated woodpecker (*Dryocopus lineatus*) stayed in the place and vocalised, or we only just heard the vocalisation. Species of the Corvidae family may exhibit escape behaviour [22]. However, in this study, six individuals of the white-throated magpie-jay attacked. They were observed foraging on the top of the trees, at about 20 m from the stimuli. When they detected the vocalisation of the collared forest-falcon, they began to vocalise stronger and continuously. They gradually approached until reaching the horn and the visual stimulus of the predator. In this flock, there was an individual who was ahead of the others. The other five individuals repeated the movements of this bird until they identified the visual stimulus and began to attack. We observed 59 behavioural responses to both predators from brown and green jays, including events in which they escaped, escaped and vocalised, vocalised or stayed and vocalised. The behaviour of this family indicates that it frequently has encounters with predators. If these species were close to the stimuli, they were the first to respond by increasing the sound of their vocalisations and moving continuously [22].

Migratory species represented 8% (5) of the total recorded species. Behavioural studies of migratory birds have shown that numerous species defend the transitory or tropical habitat, attacking or chasing other bird species [68]. Most of them may face a greater risk of predation while they are feeding, and it is probably easier for predators to catch them [69]. The anti-predatory behaviour of these birds is the use of vocalisations as warnings by prey birds, which are mostly short and sharp alert calls such as calls of the Swainson's thrush or the summer tanager [68]. Although we recorded behavioural events such as stillness (e.g. olive-sided flycatcher $n = 1$), escape (e.g. Swainson's thrush n = 6) and vocalisation (e.g. summer tanager n = 3), we consider a greater sampling effort to understand the different types of anti-predation behaviour of migratory species.

Predation is a dynamic mechanism that varies in time and space, in which predators need preys and preys can influence the presence and distribution of

predators. This principle implies that both prey and predator modify their behaviour or morphological features to survive. The result will depend on the specificity of the prey to the predator or of the predator to the prey and may result in population coexistence or decline [9]. Another result would be that predator and prey use search/capture or defence mechanisms, which over time could lead to the divergence of ecological characteristics [70]. The vocal behaviour of bird species in the El Ocote forest could be modified over time, implying new mechanisms in the communication among individuals.

### 4.2 Similarity of potential prey regarding the frequency of temporal response behaviours

In March and April, we observed most behavioural events for both predators. During the breeding season, males emit vocalisations for courtship purposes that make them more apparent to potential predators, although the benefit of this is to attract their mates or to alienate other males from their territories [9, 71, 72]. Also, in these months, there could be a greater availability of food resources, and therefore, most birds breed during this time; to protect and teach their offspring, they respond to the presence of a predator [9]. In Emilio Rabasa Ejido, prey species showed variations in their responses, the site and the moment where it was detected, so that the presence of a predator influenced foraging decisions of the prey. Species may reduce foraging time to avoid an attack, perform group observations or control group size [64].

The predation mechanism can cause variations in dispersal distances of prey birds during the chicks' care season. Predation events can create a selective advantage for dispersal [73]. Prey species could acquire, through evolutionary time, distinct types of ecological niches that are relatively free of predation pressure to allow their reproduction and survival [70]. Some prey species face a higher risk of predation than others, for instance at sites that are used by predators [69]. However, more studies are needed to understand how prey species face risks of predation during various times and seasons in the year.

### 4.3 Frequency of response behaviour events in relation to the size of potential preys

Based on the frequency of reported vocal events, we suggest that smaller species are at greater risk of predation than large ones. Small-sized bird species may be easier to capture because they are relatively more abundant than large species. However, it would be important to also consider the vegetation structure, such as the height of the trees in which they feed, combined with exposure to predators, or when species feed in groups [69].

If prey size is similar to their predators, preys would be at a disadvantage when trying to escape because they may have difficulty locating the canopy and could easily be followed by a predator [22, 34]. A lower vegetation density influences which prey can use certain strata of the vegetation. For example, small birds can more often use medium strata and thin branches to escape [22]. For some small species, the strategy of staying in groups has an important advantage such as group young care, social learning for foraging strategies, as well as increased protection and the increased possibility of escaping from a predator [74]. However, individual observation levels in large groups tend to decrease [64, 75, 76]. The cost of monitoring increases in individuals with a high probability of being depredated, such as small species [69]. In this study, small-sized species such as

the red-throated ant-tanager, the masked tityra and the boat-billed flycatcher showed behaviours such as monitoring, approaching and vocalising or attacking the stimulus. This indicates that these species could be depredated by the black-and-white owl and the collared forest-falcon and responded to the stimuli as a defence to a threat.

## 4.4 Vegetation variables and behavioural events

The probability that a prey responded to the stimuli of a predator was related to the vegetation structure (canopy height and number of live or dead trees) and the landscape (presence or absence of a water source, open area and secondary vegetation) in 36 and 37%, respectively. The arboreal vegetation functions as a shelter for prey against predators, although there are predators such as *Micrastur* species that hunt within the forest [34]. In dense vegetation, medium and large preys could not move quickly, and in the secondary forest, they would find little protection [22]. In territories with dense vegetation, small preys, such as the rufous-and-white wren (*Thryophilus rufalbus*) and the banded wren (*T. pleurostictus*), depend on acoustic rather than visual signals [77].

Birds use sites where they can maximise the diffusion range of their song, although the energy costs of singing and the warning of their presence to the predators are neglected [78]. Vocalisations may increase in environments with dense vegetation, while in open environments, they may decrease. In the first situation, species could be more exposed to intense predation, since predators use hearing to locate their prey [25, 28, 77].

Species of the Trogonidae family live in secondary forests and open areas with scattered trees. They perch in the canopy of the trees and are solitary, although sometimes they form groups for feeding in fruit trees or during the courtship season. However, the gartered trogon is widely distributed in southern Mexico and Central America and tolerates environmental changes. Trogons respond to the presence of owls by emitting sharp and crisp notes and by slowly raising their tails [79]. The black-and-white owl as a potential predator is also associated with secondary forests [45], and vegetation attributes such as canopy height and basal area of trees [69] might explain vocal recognition by prey. Understanding anti-predatory behaviour in birds is important to understand how predators influence ecological systems. Behavioural responses of birds to predation (e.g. stillness, escaping, vocalising and attacking) could be related to the physical structure of the environment; in this sense, the landscape type may influence the risk of predation.

## 5. Conclusions

Understanding the co-evolution of interacting species is one of the major challenges in the study of ecological systems. For example, studies on interactions between prey and predators and competition for resources should be realized in an ecological time scale comparable to the life of organisms [80]. The ability of birds to use signals is useful for assessing the risk of predation and provides guidelines for understanding bird behaviour, but it is also important

to study the ecological and evolutionary role of predator detection by prey. Results suggest that potential preys modify their behaviour depending on the species, where they are at that moment, the age of individuals, season, climate and previous experiences with predators, creating a behaviour that permits the potential prey to detect or evade a predator. One application of our study in the field of conservation biology and ethology would be to determine connectivity in increasingly fragmented landscapes and to use the behaviour of prey birds and their predators as a model to improve our understanding of this prey-predator mechanism in tropical ecosystems.

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## Conflict of interest

The authors declare that they have no conflict of interest.

## Compliance of ethical standards

Our study included field auditory and visual detection of 68 bird species in response to 3-minute playback of predator vocalisations. This methodology was used only to collect data for the purposes of this study, and we are aware of the consequences for the reproduction or welfare of the birds. Our research did not require the approval of any Local Ethics Committee in Chiapas, but rather of the Ethics Committee for Research of ECOSUR. The study was carried out in accordance with Mexican legislation and the authorizations given by administrative personnel of the Selva El Ocote Reserve (National Commission of Natural Protected Areas) and inhabitants of the Emilio Rabasa Ejido. Datasets analysed during the present study are available upon reasonable request to the corresponding author.

## A. Number of responses of bird species after stimuli (auditory-visual) of two potential predators

The taxonomic classification is based on the list of the American Ornithologists' Union (AOU, 2016).

| Order | Family | Scientific Name | English Name | NOM | *Ciccaba nigrolineata* (No. of responses) | *Micrastur semitorquatus* (No. of responses) |
|---|---|---|---|---|---|---|
| Tinamiformes | Tinamidae | *Crypturellus boucardi* | Slaty-breasted Tinamou | A | - | 1 |
| Galliformes | Cracidae | *Ortalis vetula* | Plain Chachalaca | | 3 | 5 |
| | Odontophoridae | *Odontophorus guttatus* | Spotted Wood-Quail | PR | 2 | 1 |
| Columbiformes | Columbidae | *Leptotila verreauxi* | White-tipped Dove | | - | 3 |
| | | *Patagioenas flavirostris* | Red-billed Pigeon | | 1 | 1 |
| | | *Zenaida asiatica* *** | White-winged Dove | | - | 1 |
| Cuculiformes | Cuculidae | *Dromococcyx phasianellus* | Pheasant Cuckoo | | 2 | 2 |
| Accipitriformes | Accipitridae | *Rupornis magnirostris* | Roadside Hawk | | - | 1 |
| Strigiformes | Strigidae | *Ciccaba nigrolineata* | Black-and-white Owl | A | 13 | - |
| | | *Ciccaba virgata* | Mottled Owl | | 14 | - |
| | | *Lophostrix cristata* | Crested Owl | A | 11 | - |
| | | *Megascops guatemalae* | Vermiculated Screech-Owl | | 4 | - |
| Trogoniformes | Trogonidae | *Trogon citreolus* ** | Citreoline Trogon | | - | 1 |
| | | *Trogon collaris* | Collared Trogon | PR | 2 | 2 |
| | | *Trogon massena* | Slaty-tailed Trogon | A | 2 | - |
| | | *Trogon caligatus* | Gartered Trogon | | 14 | 16 |
| Coraciiformes | Momotidae | *Momotus lessonii* | Lesson's Motmot | | 11 | 8 |
| Piciformes | Ramphastidae | *Aulacorhynchus prasinus* | Emerald Toucanet | PR | 1 | - |
| | | *Pteroglossus torquatus* | Collared Aracari | PR | - | 1 |
| | | *Ramphastos sulfuratus* | Keel-billed Toucan | A | 37 | 42 |
| | Picidae | *Campephilus guatemalensis* | Pale-billed Woodpecker | PR | 1 | 1 |
| | | *Dryocopus lineatus* | Lineated Woodpecker | | 1 | 2 |
| Falconiformes | Falconidae | *Micrastur ruficollis* | Barred Forest-Falcon | PR | 2 | - |
| | | *Micrastur semitorquatus* | Collared Forest-Falcon | PR | 14 | 26 |
| Passeriformes | Thamnophilidae | *Thamnophilus doliatus* | Barred Antshrike | | - | 1 |
| | Furnariidae | *Dendrocincla anabatina* | Tawny-winged Woodcreeper | PR | 3 | 1 |
| | | *Dendrocincla homochroa* | Ruddy Woodcreeper | | - | 1 |
| | | *Lepidocolaptes souleyetii* | Streak-headed Woodcreeper | | 1 | - |
| | | *Sittasomus griseicapillus* | Olivaceous Woodcreeper | | 3 | 2 |
| | | *Xiphorhynchus flavigaster* | Ivory-billed Woodcreeper | | 6 | 2 |
| | Tyrannidae | *Attila spadiceus* | Bright-rumped Attila | | 13 | 1 |
| | | *Contopus cooperi* *** | Olive-sided Flycatcher | | 2 | - |
| | | *Megarynchus pitangua* | Boat-billed Flycatcher | | 3 | 2 |
| | | *Myiarchus tuberculifer* | Dusky-capped Flycatcher | | 1 | 3 |
| | | *Myiozetetes similis* | Social Flycatcher | | 1 | 11 |
| | | *Oncostoma cinereigulare* | Northern Bentbill | | 8 | 5 |
| | | *Onychorhynchus coronatus* | Royal Flycatcher | P | 3 | 2 |
| | Tityridae | *Pachyramphus major* | Gray-collared Becard | | - | 1 |
| | | *Schiffornis veraepacis* | Northern Schiffornis | | 1 | - |
| | | *Tityra semifasciata* | Masked Tityra | | 3 | 6 |
| | Cotingidae | *Lipaugus unirufus* | Rufous Piha | | 2 | 5 |
| | Pipridae | *Chiroxiphia linearis* | Long-tailed Manakin | PR | 6 | 18 |
| | Vireonidae | *Cyclarhis gujanensis* | Rufous-browed Peppershrike | | - | 1 |
| | | *Pachysylvia decurtata* | Lesser Greenlet | PR | 2 | 5 |
| | | *Vireo flavoviridis* | Yellow-green Vireo | | 4 | 1 |
| | | *Vireolanius pulchellus* | Green Shrike-Vireo | A | 4 | 4 |
| | Corvidae | *Calocitta formosa* | White-throated Magpie-Jay | | - | 15 |
| | | *Cyanocorax yncas* | Green Jay | | 9 | 17 |
| | | *Psilorhinus morio* | Brown Jay | | 11 | 22 |
| | Troglodytidae | *Henicorhina leucosticta* | White-breasted Wood-Wren | | 17 | 7 |
| | | *Pheugopedius maculipectus* | Spot-breasted Wren | | - | 4 |
| | | *Thryophilus pleurostictus* | Banded Wren | | - | 1 |
| | Turdidae | *Catharus ustulatus* *** | Swainson's Thrush | | 6 | 6 |
| | | *Turdus grayi* | Clay-colored Thrush | | 2 | - |
| | Fringillidae | *Euphonia hirundinacea* | Yellow-throated Euphonia | | 1 | 1 |
| | Parulidae | *Basileuterus lachrymosus* | Fan-tailed Warbler | | 1 | 1 |
| | | *Setophaga magnolia* *** | Magnolia Warbler | | 1 | - |
| | Thraupidae | *Cyanerpes cyaneus* | Red-legged Honeycreeper | | 8 | 9 |
| | Emberizidae | *Aimophila rufescens* | Rusty Sparrow | | - | 1 |
| | | *Arremonops rufivirgatus* * | Olive Sparrow | | 2 | 4 |
| | Cardinalidae | *Caryothraustes poliogaster* | Black-faced Grosbeak | | 1 | - |
| | | *Habia fuscicauda* | Red-throated Ant-Tanager | | 10 | 8 |
| | | *Habia rubica* | Red-crowned Ant-Tanager | | 6 | 5 |
| | | *Piranga rubra* *** | Summer Tanager | | 2 | 2 |
| | Icteridae | *Amblycercus holosericeus* | Yellow-billed Cacique | | 1 | 2 |
| | | *Dives dives* | Melodious Blackbird | | - | 1 |
| | | *Molothrus aeneus* | Bronzed Cowbird | | - | 1 |
| | | *Psarocolius montezuma* | Montezuma Oropendola | PR | - | 2 |
| | | **Total of species** | | | 51 | 55 |
| | | **Total of responses** | | | 279 | 295 |

\* Cuasiendemic, ** Endemic, *** Migratory; A= Threatened, Pr= Special Protection, blank= no category. − No records

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