ANTI-PREDATOR RESPONSES OF NEOTROPICAL RESIDENT AND MIGRANT BIRDS TO FAMILIAR AND UNFAMILIAR OWL VOCALIZATIONS ON THE YUCATAN PENINSULA

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Resumen. – Comportamiento de evasión de depredadores de aves Neotropicales residentes y migratorias a vocalizaciones de lechuzas familiares y no familiares en la Península de Yucatán. – Para reducir el riesgo de depredación, los animales necesitan utilizar estrategias de detección de depredadores efectivas. Muchas especies dependen de su experiencia previa, o de aprendizaje, para detectar el riesgo de depredación, pero esta estrategia es inefectiva cuando estas especies son expuestas a un depredador potencial que no les es familiar. Sin embargo, varias especies exhiben un comportamiento innato a depredadores potenciales pero, hasta donde sabemos, ningún estudio ha examinado el comportamiento de aves hacia especies alopátricas de depredadores que no son familiares. En el presente estudio expusimos aves tropicales migratorias y residentes en la Península de Yucatán, México, a vocalizaciones de dos especies de lechuza: el residente Tecolote Bajeño (*Glaucidium brasilianum*), el cual se asume que es familiar a ambos grupos migratorios y residentes, y un autillo alopátrico norteamericano Tecolote Chillón (*Megascops asio*), el cual probablemente solo es familiar al grupo migratorio que se reproduce en zonas templadas del este de Norteamérica. La mayoría de aves únicamente respondieron a las vocalizaciones de depredador que se esperaba fuera familiar: ambos grupos migrantes y residentes respondieron vigorosamente al tecolote bajeño; el autillo solo elicitó comportamiento de las aves migrantes. Estos resultados indican que las aves residentes no tienen la habilidad de reconocer de forma innata, o de deducir peligro, de las vocalizaciones de depredadores nuevos. Así mismo que se expanden las distribuciones de especies, y depredadores exóticos se introducen en áreas nuevas, aumentará en importancia el entendimiento de capacidad y estrategias de reconocimiento de depredadores en especies de presa.

Abstract. – To reduce predation risk, animals must employ effective predator-detection strategies. Many species rely on prior experience, or learning, to detect predation risk, but this strategy is ineffective when exposed to an unfamiliar potential predator. Many species, however, exhibit an innate response to potential predator species but to our knowledge, no studies have examined the response of birds to unfamiliar, allopatric predator species. In this study, we exposed migrant and resident tropical birds on the Yucatan Peninsula, Mexico, to vocalizations of two owl species: the resident Ferruginous Pygmy-owl (*Glaucidium brasilianum*), assumed to be familiar to both migrants and residents, and the allopatric Eastern Screech-owl (*Megascops asio*), likely to be familiar only to migratory birds that breed in eastern temperate North America. Most birds responded only to predator vocalizations with which they were expected to be familiar: both migrants and residents responded strongly to Ferruginous Pygmy-owl vocalizations; the Eastern Screech-owl vocalization elicited a response only from migrants. These results suggest that tropical residents are

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unable to recognize innately, or to infer danger from, vocalizations of novel predators. As species ranges expand and exotic predators are introduced to new areas, it will be important to better understand the predator recognition response of potential prey species. *Accepted 31 July 2007.*

INTRODUCTION

Predator detection is crucial for reducing an animal's predation risk (Lima & Dill 1990, Caro 2005). Many species rely on experience with a predator to facilitate recognition (Mirza *et al.* 2006). However, innate recognition of predators has been demonstrated repeatedly in taxa as diverse as desert pocket mice (*Chaetodipus pencillatus*, Punzo 2005), Atlantic salmon (*Salmo salar*, Hawkins *et al.* 2004), American toads (*Bufo americanus*, Gallie *et al.* 2001) and many species of birds (e.g., Veen *et al.* 2000, Goth 2001, Wiebe 2004). Notably, these and other similar studies have examined responses by prey to only sympatric species. Very few studies (e.g., Blumstein *et al.* 2000, Veen *et al.* 2000) have examined the response to an allopatric, unfamiliar predator species.

Some prey species respond to visual stimuli of a foreign predator (Blumstein *et al.* 2000, Veen *et al.* 2000). However, predators are not always visible; sometimes the only evidence of their presence may be auditory. Some species recognize and respond to audible cues produced by predators (e.g., birds: Miller 1952, Hauser & Caffrey 1994, Hakkarainen *et al.* 2002, Rainey *et al.* 2004, and mammals: Swaisgood *et al.* 1999, Gil-da-Costa *et al.* 2003). To our knowledge, only the study by Blumstein *et al.* (2000) has examined the response to auditory cues of allopatric, unfamiliar predators: in that study, tammar wallabies (*Macropus eugenii*) responded to visual, but not auditory, stimuli of both novel and familiar predatory species. The generality of this result to other animal groups remains to be tested. This is essential to our understanding of the mechanisms of predator recognition: we need to know which cues are pertinent to certain animal groups and the circumstances under which they are important.

When encountering potential predators, individuals can restrict their response to only those species with which they are familiar. Conversely, they may use internal cues (autonomous neuropsychological processes) to presume an unfamiliar predator species is dangerous. Indeed, such internal cues have helped some predator-naïve populations of red-necked pademelons (*Thylogale thetis*) to survive introductions of exotic predators (Blumstein *et al.* 2002). We predict that if individuals need to maximize awareness of predatory hazards, most should use internal cues to respond to threat signals regardless of previous experience, and few will restrict their responses to only those signals with which they are familiar. To test this prediction, we deployed songs of a familiar and an unfamiliar predatory owl species and monitored the response of over-wintering migrant and resident Neotropical birds at a study site in the Yucatan Peninsula of Mexico. We chose to use auditory cues of owls because they generally vocalize en route to their hunting perches, providing a reliable indicator of local owl activity (Hendrie *et al.* 1998). These auditory cues are also appropriate because small owls tend to produce high-pitched staccato vocalizations (Miller 1934, 1947), which makes members of this group generally easy to recognize by sound and creates appropriate circumstances to detect responses from internal cues. This design avoids potential biases created by using entirely out-of-context sounds.

We used the Eastern Screech-owl (*Megascops asio*) as our allopatric exemplar. It is a small owl that commonly depredates passerines (Gehlbach & Leverett 1995). It is widespread east of the Rocky Mountains from Canada to northern Mexico (Gehlbach 1995). The Eastern Screech-owl's range does not extend south into the Yucatan Peninsula and its song would therefore be a novel vocalization to the resident species of the Yucatan. Eastern Screech-owls have two distinct songs, a monotonic trill and a descending trill (Gehlbach 1995). Passerines that breed in eastern North America (including the majority of migratory birds at our study site) should be familiar with the vocalization and respond to the screech-owl's monotonic trill (Gehlbach & Leverett 1995).

The Ferruginous Pygmy-owl (*Glaucidium brasilianum*) is a small owl that is also an important predator of passerines (Proudfoot 1997); it is abundant and distributed widely across the tropical lowlands of Mexico (Proudfoot & Johnson 2000). Ferruginous Pygmy-owls are numerous and conspicuous at our study site, so we are confident most birds in the area had been exposed to their song. The Ferruginous Pygmy-owl's song (also described as a call, e.g., Proudfoot & Johnson 2000) is a series of hollow whistles, sometimes ending with high, yelping twitters (Howell & Webb 1995); it is imitated commonly by birders both to attract pygmy-owls and elicit a response from songbirds and has been used to assist point-counts in the Yucatan (Lynch 1989).

If resident birds of the Yucatan can recognize vocalizations innately, then there should be no difference in their response to the unfamiliar screech-owl and the familiar pygmy-owl. This is the same pattern we would expect from Neotropical migrants overwintering in the area, who should be familiar with both. Conversely, if resident birds of the Yucatan do not innately recognize predator vocalizations, then there should be a biased response toward the familiar pygmy-owl.

METHODS

To test our predictions, observations and playbacks were conducted from 3–7 March 2004 in deciduous dry forest adjacent to the Centro Ecologico Akumal in Akumal, Yucatan, Mexico. Four study sites, roughly 200 m apart, were chosen for this experiment based on vegetation composition and accessibility. This distance is adequate to provide us with independent samples; several studies (e.g., Sliwa & Sherry 1992, Confer & Holmes 1995) have shown that sites separated by >100 m effectively eliminated double-counting in vegetated Neotropical habitats, and in such habitats, sound from playbacks (~75 Db) should quickly attenuate to background noise by 100 m. Two sites were within forest, while the other two were in a 15 m-wide telephone line right-of-way dominated by scrub and edge vegetation.

Experiments consisted of providing owl song playback for 150 s followed by 30 s of silence. This pattern was repeated three additional times for each trial. Each playback was preceded with 2 min of silence and followed with 7 min of silence. Total playback trial duration was 21 min. The Eastern Screech-owl playback was of a 1 min recording of their monotonic trill (cycled continuously). The Ferruginous Pygmy-owl playback was of a 20 s recording of their repeated song (cycled continuously). Because our study design only incorporated one repeated song for each playback, we used linear mixed-effects models (see below) to reduce the effect of potential pseudo-replication by accounting for random error associated with sampling design. We played songs at a constant volume using an iPod mini (Apple Computer, Inc.) attached to a speaker (Saul Mineroff Electronics, Inc.) on the ground in the site center. Because of a lack

of control, we tested only the directionality of response, rather than the strength of the response.

Playbacks were alternated between sites, and were restricted to 06:00–12:00 and 14:00–17:00 h, to capture the peak activity period (Poulsen 1996). Each day, the order of sites visited and songs played varied from the previous day so that all sites were visited in a different order and time of day. Overall, 15 playback trials were conducted using Eastern Screech-owl song and 15 using Ferruginous Pygmy-owl song (edge site 1: 4 screech-owl, 3 pygmy-owl; edge site 2: 4 screech-owl, 4 pygmy-owl; forest site 1: 4 screech-owl, 4 pygmy-owl; forest site 2: 3 screech-owl, 4 pygmy-owl).

All individuals responding to playbacks were recorded throughout the trial, including the pre- and post-treatment silence periods. We considered birds to be responding if they exhibited the following behaviors: agitation, chipping, calling, flying in to the speaker, or attacking a Ferruginous Pygmy-owl that had responded to the playback (which occurred in 73% of the trials in which a Ferruginous Pygmy-owl song was played). Those birds passing through the site without responding or showing interest in the speaker were deemed "passers-by" and not used in the subsequent analyses.

Because most observed birds were actively responding to the playback, we could not use a binary response variable (responding, not responding) to control for species abundance. Instead, we built linear mixed-effects models (LME), using *R* v. 2.1.1 (R Development Core Team 2005) to assess whether the absolute number of respondent migrants and residents differed between owl-song treatments ($\alpha = 0.05$), and the direction of those relationships. The psuedoreplicated structure of our experiments yields a small effective sample size. To contend with this, we chose LME for our analyses because it

accounts for the non-independence of errors created by spatial and temporal pseudoreplication. LME simultaneously estimates how variables influence the mean (fixed effects) and predicts how within-group correlation (random effects related to sampling design, such as the use of playback song from a single individual) influences the variance (Crawley 2005). As predictive variables, we used a binary treatment classification (Eastern Screech-owl vs Ferruginous Pygmy-owl) as a fixed effect, and included time-of-day, nested within site (to weight for within-group errors), as a random effect. We compared variance components to assess model fit.

We differentiated between migrant and resident species with the classifications used by Lynch (1989). We then tested for detectable differences in the number of individual migrants ("all-migrant" model) vs residents ("all-resident" model). To examine patterns more closely, we then built species-specific models for the most commonly detected species: Yucatan Jay (*Cyanocorax yucatanicus*; resident), Yucatan Vireo (*Vireo magister*; resident), Mangrove Vireo (*V. pallens*; resident), White-eyed Vireo (*V. griseus*; migrant), and Melodious Blackbird (*Dives dives*; resident).

We expected that if a playback type was associated with a greater number of individuals in the all-migrant and all-resident models, it should also be associated with a greater number of species. In other words, within each migratory group (i.e., migrants or residents), we sought to determine which song elicits a response from the most species. Because we lacked the appropriate degrees of freedom to construct LME models (migrant species abundance per trial ranged from 0–3), we instead used Wilcoxon non-parametric tests to examine this; if our expectation were not supported (indicating the medians were drawn from the same distribution), it would reveal important species-specific bias in our results.

TABLE 1. Number of individuals of each species responding to playbacks from Eastern Screech-owls (EASO) and Ferruginous Pygmy-owls (FEPO). Migratory status of each species is denoted as M (Migrant) or R (Resident), as classified by Lynch (1989).

Common names	Scientific names	EASO	FEPO	Status
Black Catbird	*Melanoptila glabrirostris*	0	1	R
Black-cowled Oriole	*Icterus prosthemelas*	0	1	R
Blue Bunting	*Cyanocompsa parellina*	3	1	R
Buff-bellied Hummingbird	*Amazilia yucatanensis*	0	2	R
Canivet's Emerald	*Chlorostilbon canivetii*	0	1	R
Caribbean Elaenia	*Elaenia martinica*	0	1	R
Cinnamon Hummingbird	*Amazilia rutila*	2	8	R
Common Yellowthroat	*Geothlypis trichas*	0	1	M
Golden-fronted Woodpecker	*Melanerpes aurifrons*	0	2	R
Gray Catbird	*Dumetella carolinensis*	1	1	M
Great-tailed Grackle	*Quiscalus mexicanus*	0	2	R
Hooded Oriole	*Icterus cucullatus*	1	3	R
Great Kiskadee	*Pitangus lictor*	5	1	R
Magnolia Warbler	*Dendroica magnolia*	4	5	M
Mangrove Swallow	*Tachycineta albilinea*	0	1	R
Mangrove Vireo	*Vireo pallens*	1	12	R
Melodious Blackbird	*Dives dives*	2	12	R
Orange Oriole	*Icterus auratus*	0	1	R
Ovenbird	*Seiurus aurocapilla*	1	0	M
Rose-throated Becard	*Pachyramphus aglaiae*	0	2	R
Rufous-browed Peppershrike	*Cyclarhis gujanensis*	0	1	R
Social Flycatcher	*Myiozetetes similis*	0	11	R
Spot-breasted Wren	*Thryothorus maculipectus*	1	3	R
Tropical Kingbird	*Tyrannus melancholicus*	0	4	R
Tropical Mockingbird	*Mimus gilvus*	0	1	R
White-eyed Vireo	*Vireo griseus*	5	10	M
White-winged Dove	*Zenaida asiatica*	0	2	R
Yellow-throated Warbler	*Dendroica dominica*	0	2	M
Yucatan Jay	*Cyanocorax yucatanicus*	2	46	R
Yellow-lored Parrot	*Amazona xantholora*	0	2	R
Yucatan Vireo	*Vireo magister*	0	31	R

RESULTS

Few individuals were detected in the pre-playback period (18 total) and no individuals were behaving in such a way as to be considered "respondents" prior to playbacks. Individuals present in the pre-playback period were therefore only included in subsequent analyses if they flew in toward the speaker and a mobbing response was

elicited. Of the 170 resident birds that responded to playback, 152 birds (representing 27 species) responded to Ferruginous Pygmy-owl song and 18 birds (9 species) responded to Eastern Screech-owl song. Of the 31 migratory birds that responded to playback, 11 (5 species) responded to Eastern Screech-owl song, while 20 (6 species) responded to Ferruginous Pygmy-owl song. All species responding to play-

TABLE 2. Linear mixed-effects models describing abundance of migrants, residents, and the five species most commonly detected at playbacks of Eastern Screech-owl and Ferruginous Pygmy-owl songs in Aku-mal, Mexico. As predictive variables, a binary treatment classification (screech-owl vs pygmy-owl) was used as a fixed effect, and time-of-day (nested within site) was used as a random effect. Comparison of SD of the random-effect and intercept-only models estimates the time-of-day influence. T-value indicates strength of relationship between abundance and treatment type; except for White-eyed Vireo, abundance in all models was positively related to playbacks of Ferruginous Pygmy-owl.

Species/group	SD intercept-only	SD random-effect model	t-value	P
All-migrants	1.29	0.001	1.94	0.06
All-residents	2.16	0.0003	9.50	< 0.0001
Mangrove Vireo	0.37	0.0005	4.51	0.0001
Melodious Blackbird	0.94	0.001	2.05	0.05
White-eyed Vireo	0.01	0.0002	1.91	0.07
Yucatan Jay	0.99	0.001	2.45	0.02
Yucatan Vireo	1.06	0.001	9.19	< 0.0001

backs and their migratory status are listed in Table 1.

The overall number of residents was strongly related to playback type; however, response by migrants was less marked (Table 2). All residents were positively associated with playbacks of Ferruginous Pygmy-owls. This relationship is especially apparent in the resident species-specific models for Man-grove Vireo, Melodious Blackbird, Yucatan Jay, and Yucatan Vireo (Table 2). Migrant response did not differ between playback types (Figure 1); however the White-eyed Vireo was positively associated with Eastern Screech-owl playback in the species-specific model (Table 2). The random effects of time-of-day were negligible across sites for both the all-resident and all-migrant models com-pared to the intercept-only model (Table 2), therefore there is no important effect of within-group (time-of-day | site) error from temporal and spatial pseudoreplication on the covariance structure of the data (i.e., errors are independent).

There was no significant difference in the number of migrant species responding to Fer-ruginous Pygmy-owl playbacks as compared to Eastern Screech-owl playbacks (Wilcoxon

test: $Z = -1.348$, $P = 0.18$). The number of resident species responding to Ferruginous Pygmy-owl playbacks was significantly higher than the number of resident species respond-ing to Eastern Screech-owl playbacks (Wil-coxon test: $Z = -4.278$, $P < 0.001$; Fig. 1).

DISCUSSION

Our results reveal an important component of the predator recognition process: birds responded to vocalizations of predator spe-cies that they recognized. Migrant and resi-dent tropical birds responded to familiar songs of the Ferruginous Pygmy-owl. How-ever, migrants responded more strongly to the vocalizations of the Eastern Screech-owl than did tropical resident birds.

Because they produce distinctive vocal-izations (Miller 1934, 1947), most small owls can be recognized audibly. Accordingly, it could be expected that Neotropical resi-dents would respond equally to the famil-iar pygmy-owl and the novel screech-owl songs. However, our results do not support this expectation. Instead our results suggest that birds tend to respond to threat cues with which they are experi-
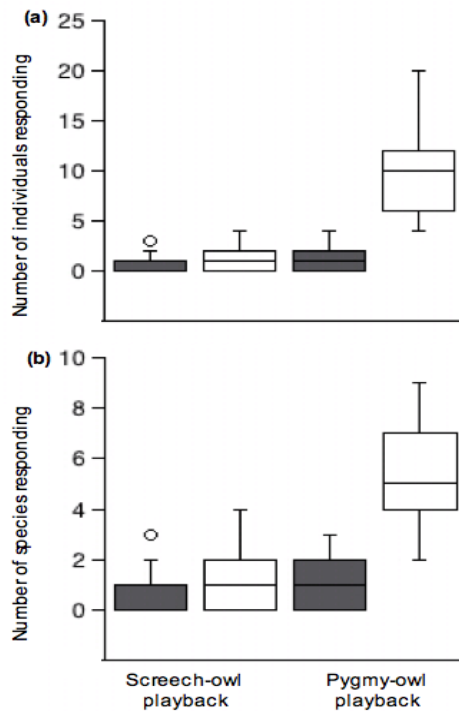
FIG 1. Box plots of the number of individuals (A) and species (B) responding to Eastern Screech-owl (n = 15) and Ferruginous Pygmy-owl (n = 15) playbacks. Gray boxes represent Neotropical migrants, open boxes represent species resident to the Yucatan Peninsula. Box plots show the median, 10th, 25th, 75th, and 90th percentiles with horizontal lines. Data points outside this range are represented by open circles.

enced, and do not infer danger from unfamiliar sounds.

An alternate explanation for our results, which our data cannot refute, is that the Neotropical residents did not respond to the screech-owl playback due to 'neophobia' (e.g., fear of a new sound in the area). This explanation is plausible because migrants tend to show greater exploratory behavior and less neophobia than non-migrants (Mettke-Hofmann & Gwinner 2004). However, this is a less parsimonious explanation than our argu-

ments regarding recognition; susceptibility to neophobia differs between species even within closely related taxonomic groups (Mettke-Hofmann *et al.* 2002, Reader 2003) and it therefore is unlikely to simultaneously afflict such a large group of species as resident birds of the Yucatan.

Resident bird species have presumably never had contact with an Eastern Screech-owl and therefore have not learned the level of threat it poses. The finding that some resident species did respond to the Eastern Screech-owl playback (Table 1), however, suggests that some species may have an innate response to owl vocalizations, or aspects of the vocalizations shared with familiar owl species, and warrants further investigation. One explanation that we cannot rule out, and would be clarified by additional playback studies, is that the Eastern Screech-owl song may be similar enough to that of a resident congeneric species, the Vermiculated Screech-owl (*M. guatemalae*), to elicit an anti-predator response. Vermiculated Screech-owls, whose songs also constitute monotonic trills, are widespread in the Yucatan (Howell & Webb 1995) and we observed several within 5 km of our study site, although we did not detect any at the site itself.

Although we provide evidence that birds in our study only responded to predator vocalizations with which they were familiar, the generality of this finding is unclear. Mixed-species flocks in tropical forests often vary in size, composition, and dynamics depending on latitude and habitat type (Poulsen 1996). Undoubtedly, other communities may show different response patterns because they face predation threats that exert different types of selective influence. For instance, many tropical environments have pronounced dry and wet seasons causing several species to move widely between seasonal resource patches (Fogden 1972, Thiollay

2002), which creates a constantly changing predation landscape. Predator recognition in these systems may require a different process than we observed in the Yucatan.

Another possible explanation is that the initiation of a mobbing response by migrant species may trigger a mobbing response by the residents, as observed among Black-capped Chickadees (*Poecile atricapillus*, Hurd 1996, Turcotte & Desrochers 2002) and other species (Forsman & Mönkkönen 2001). Our data do not allow investigation of this hypothesis or to estimate the role and direction of information transfer between heterospecifics; one group of species may respond more or less eagerly when parasitizing the information (e.g., mobbing behavior indicating a predator's location) provided by heterospecifics in another group. However, playbacks can be a valuable tool for elucidating individual species' roles in mixed-species flocks (Goodale & Kotagama 2005). The migratory White-eyed Vireo was the most common respondent to Eastern Screech-owl playbacks, responding in 33% of trials. Although a common respondent, we found no evidence from the literature that White-eyed Vireos (or any species for which we constructed separate models) act as sentinel species, though we suggest its potential role in mobbing response warrants further investigation.

We have shown that many bird species in the Yucatan failed to recognize the sounds of an exotic predator. However, other studies have demonstrated that some animals can respond appropriately to exotic predatory threat (Blumstein *et al.* 2002). This highlights the importance of identifying the species most vulnerable to invasive or introduced predators, a particularly common phenomenon in the tropics. There is ample opportunity to study this, even outside dynamic tropical communities. For instance, the Barred Owl (*Strix varia*) is rapidly expanding its range westward in North America (Dark *et*

al. 1998), creating not only competition for the congeneric Spotted Owl (*S. occidentalis*), but also constituting a novel predatory threat to small bird and mammal species in areas it invades. We predict that some species will effectively discriminate between, and respond to, such sympatric and evolutionarily allopatric predators.

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