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Sensory-based niche partitioning in a multiple predator–multiple prey community

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Many predators and parasites eavesdrop on the communication signals of their prey. Eavesdropping is typically studied as dyadic predator–prey species interactions; yet in nature, most predators target multiple prey species and most prey must evade multiple predator species. The impact of predator communities on prey signal evolution is not well understood. Predators could converge in their preferences for conspicuous signal properties, generating competition among predators and natural selection on particular prey signal features. Alternatively, predator species could vary in their preferences for prey signal properties, resulting in sensory-based niche partitioning of prey resources. In the Neotropics, many substrate-gleaning bats use the mate-attraction songs of male katydids to locate them as prey. We studied mechanisms of niche partitioning in four substrate-gleaning bat species and found they are similar in morphology, echolocation signal design and prey-handling ability, but each species preferred different acoustic features of male song in 12 sympatric katydid species. This divergence in predator preference probably contributes to the coexistence of many substrate-gleaning bat species in the Neotropics, and the substantial diversity in the mate-attraction signals of katydids. Our results provide insight into how multiple eavesdropping predator species might influence prey signal evolution through sensory-based niche partitioning.

1. Introduction

Eavesdropping on the communication signals of other species is common across diverse taxa and sensory modalities [1,2]. Animals that produce signals to attract mates experience conflicting selection pressures acting on different components of fitness: increased conspicuousness to mates also increases conspicuousness to predators [1]. The majority of work on such conflicts has focused on single predator–prey species interactions, but in nature a diversity of prey interacts with a diversity of predators. Theory and empirical evidence support the idea that multiple predator species can have effects on prey communities that are not readily apparent by studying a single dyadic predator–prey interaction [3]. It has been proposed that more detailed analyses of predator behaviour could contribute to a better understanding of predator–prey dynamics [3,4]. If most predators in a community select prey based on similar prey signal features, such as specific visual or acoustic wavelengths, we would expect prey species to converge on a signal that optimizes defence while maintaining attractiveness to mates. Conversely, diverse predator hunting strategies could lead to variation in signal design and defence strategies. In the latter case, the result might depend on sensory-based differences in eavesdropping behaviour between predator species.

We examined which of these two scenarios exists in the multi-predator–multi-prey community of Neotropical gleaning bats and katydids. In the

Neotropics, katydids are an important component of the diet of substrate-gleaning bats (bats that capture prey off surfaces, typically vegetation) [5–7]. A number of species of gleaning bats locate nocturnally singing katydids by eavesdropping on the mate-attraction call that males emit to attract females [5,8]. One gleaning bat species has been shown to prefer frequently repeated katydid calls over infrequent calls [5]. Although gleaning bats that eavesdrop on the mate-attraction songs of male katydids are a classic example of a predator–prey behavioural interaction, until now preference divergences across multiple predators for the acoustic features of prey signals has not been considered in the context of an evolutionary arms race between predators and prey. Katydids demonstrate a variety of anti-predator strategies [9], some of which have probably evolved in response to bat predation [10]. Some katydids that call in habitats where gleaning bats forage have been shown to produce low duty cycle calls (i.e. a low percentage of signal time occupied by sound) [5], and some even cease calling in response to bat echolocation calls [11–14]. Both of these adaptations suggest that bat predation is a major selective factor in the evolution of katydid mating behaviour.

Niche partitioning can occur through sensory [15], behavioural [16,17] and morphological mechanisms [18–20]. We evaluated five predator characteristics that could contribute to the partitioning of katydid prey within a Neotropical gleaning bat guild that incorporate these three different mechanisms: (i) species-level preferences for prey-generated sounds, (ii) echolocation call design, (iii) morphological characteristics related to flight manoeuvrability, (iv) bite force and (v) prey-handling abilities. These five features also cover the different stages of the predation sequence, from detection and localization, to attack and consumption [21]. We hypothesized that gleaning bats would prefer katydid calls with acoustic properties that are relatively easy to detect and localize. Alternatively, each bat species might prefer different acoustic characteristics of the calls of katydids, suggesting a foundation for sensory-based niche partitioning. Echolocation call design can constrain the perceptual ability of bats that navigate and forage close to vegetation, which creates acoustic clutter by masking echoes of prey [15]. Likewise, certain morphological features, such as body size, wing loading and aspect ratio, are highly correlated with flight manoeuvrability in bats [22,23]. Both call design and flight manoeuvrability might contribute to differences in the ability of gleaners to capture substrate-borne prey. Finally, differences in bite force and prey-handling could contribute to differences in the ability of gleaning bats to subdue katydid prey and therefore also correspond with bat species differences in prey preferences.

2. Material and methods

Katydid recordings were recorded between February and March 2011, and experiments with bats were conducted from February to July 2012 in Panamá at the facilities of the Smithsonian Tropical Research Institute (STRI) on Barro Colorado Island (BCI) and in Gamboa.

(a) Katydid recordings

Katydid calls were recorded for playbacks to bats and for call structure analysis. Katydids were collected at night from lights around the buildings on BCI. Calls were recorded from individual caged males with a condenser microphone (CM16; Avisoft

Bioacoustics) and an UltraSoundGate 416H A/D converter (250 kHz sampling rate; Avisoft Bioacoustics) connected to a laptop computer running Recorder software (Avisoft Bioacoustics). Acoustic parameters of katydid calls were measured with the sound analysis software SASLab Pro (Avisoft Bioacoustics; table 1). We selected calls from 12 species of katydids for playbacks to bats (figure 1). For each individual, we randomly chose a single call from a singing bout and repeated this call at the calculated average call period for each species. To determine the species-specific average call period, we first measured the onset time from one call to the onset time of the next call for all calls within an individual. Call activity varied considerably during recording, so we sorted the call period data for an individual and calculated the average of the shortest quartile (25%) of call periods to determine a mean call period for an individual while actively calling. By averaging the mean call periods across all individuals, we determined the call period for that katydid species.

To correct for the frequency response of the microphone and generate audio files with accurate power spectra, we applied a frequency response filter that was an inverse of the microphone frequency response using SASLab Pro. We used these filtered recordings for measurements of the spectral parameters of the calls. From our katydid recordings, we measured five acoustic parameters: (i) number of pulses per call, counted from the oscillogram display, (ii) summed call duration (ms), defined as the total time of all sound pulses per call, (iii) call duty cycle (%), defined as the ratio of the summed call duration divided by the total call period multiplied by 100, (iv) peak frequency (kHz), defined as the frequency with the most energy as measured from the power spectrum and (v) bandwidth (kHz), defined as the difference between the maximum and minimum call frequencies measured at -20 dB (re peak frequency).

(b) Bat responses to katydid calls

Individuals of four species of Phyllostomid gleaning bats (*Lophostoma silvicolum* $N = 14$, *Micronycteris microtis* $N = 14$, *Tonatia saurophila* $N = 11$ and *Trachops cirrhosus* $N = 7$), were captured with mistnets placed across streams in the forest or with hand-nets at roosts. Bats captured on BCI ($N = 17$) were held in a $4.5 \times 3.7 \times 2.0$ m wire mesh flight cage, while bats captured in Gamboa ($N = 29$) were held in a $5 \times 5 \times 2.5$ m wire mesh flight cage. Flight cages at both sites were outdoors, hence captured bats experienced ambient temperature, lighting and humidity. Bats were given *ad libitum* food the night before measuring their behavioural responsiveness and were released into the flight cage and allowed to acclimate for 1.5 h before testing. All bats had *ad libitum* access to water. Upon completion of the experiment a small piece of wing tissue was collected for DNA extraction for other studies, and to mark individuals to avoid resampling. All bats were released at their capture sites.

We hypothesized that gleaning bats would prefer katydid calls with acoustic properties that were easier for that bat to detect and localize. We considered five signal parameters: (i) number of pulses per call, (ii) summed duration of sound pulses per call, (iii) call duty cycle [5], (iv) call peak frequency and (v) bandwidth. We predicted that bats would prefer katydid calls with higher signal energy (i.e. more pulses per call, a longer summed duration, higher duty cycle and lower peak frequency) because we hypothesized these calls would be easier for bats to detect when they are further away from katydid prey. Likewise, we predicted that bats would prefer katydid calls with a larger signal bandwidth because they contain more information and therefore would be more likely to fall within the most sensitive hearing range and be easier to localize by gleaning bat predators [24,25].

We presented each individual bat with the calls of 12 katydid species broadcasted in random order from a ScanSpeak Ultrasound

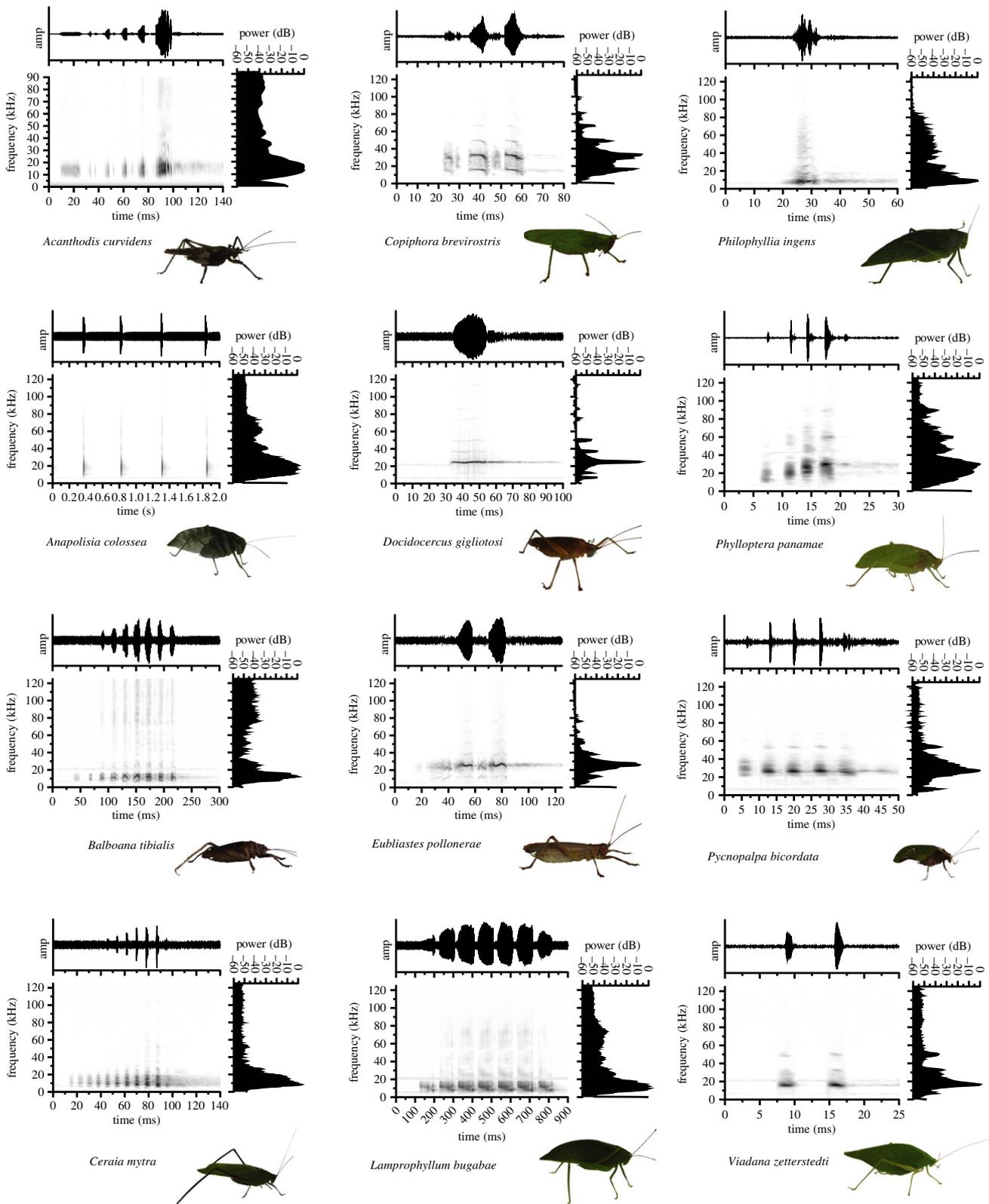


Figure 1. Katydid species and their calls used in playback experiments to bats. Plots illustrate the oscillogram (top), spectrogram (bottom, left) and power spectrum (bottom, right) of the calling song of each species. (Online version in colour.)

speaker (frequency response ± 4.5 dB between 5 and 90 kHz; Avisoft Bioacoustics) via an UltraSoundGate Player 116 using Recorder software (Avisoft Bioacoustics). The playback speaker was placed in the centre of the flight cage on a table 0.7 m above the floor. The speaker was surrounded with leaves. All calls were broadcast to bats at 100.8 dB SPL (decibels sound pressure level re 20 μ Pa). Signal amplitudes were measured at 20 cm from the loudspeaker with a CEL-414 precision impulse sound pressure-level meter. Playback stimuli contained up to 10 repeated katydid calls. The playback duration was limited to 4 min for katydid species

with low duty cycles (*Acanthodis curvidens*, *Ceraia mytra*, *Copiphora brevirostris*, *Philophyllia ingens*). Bats were given at least 2 min of silence after each katydid species' call before commencing with the playback of the next katydid species. Behavioural responses of bats to katydid playbacks were recorded using two digital camcorders with Nightshot setting (Sony Handycam DCR-SR45), illuminated with a single 25 watt red light bulb and infrared LED lights (IR045, Clover Electronics). One camera was fixed on the playback loudspeaker while the other was manually oriented to the bat being tested.

Table 1. Call parameter measurements for the 12 Neotropical katydid species used in the acoustic playback experiments. N = number of katydid individuals, one call per individual.

subfamily	species	no. pulses	duty cycle (%)	summed duration of pulses (ms)	peak frequency (kHz)	bandwidth (kHz)	N
Copiphorinae	<i>Copiphora breviostris</i>	2.8 ± 0.4	0.036 ± 0.008	18.7 ± 4.4	32.9 ± 0.7	18.8 ± 6.4	5
Phaneropterinae	<i>Anapolisia colossea</i>	5.6 ± 2.1	15.833 ± 8.046	77.2 ± 37.2	20.6 ± 1.3	18.5 ± 1.8	5
	<i>Ceraia mytra</i>	10.7 ± 0.6	0.011 ± 0.000	15.4 ± 6.1	11.5 ± 1.5	12.6 ± 2.3	3
	<i>Lamprophyllum bugabae</i>	159.6 ± 32.2	3.544 ± 0.184	96.7 ± 16.9	11.4 ± 2.1	11.0 ± 1.4	5
	<i>Philophyllia ingens</i>	1.0 ± 0.0	0.016 ± 0.008	7.0 ± 3.6	10.4 ± 1.4	3.0 ± 2.4	3
	<i>Phylloptera panamae</i>	5.0 ± 1.0	0.161 ± 0.008	3.4 ± 1.3	27.3 ± 0.7	20.1 ± 1.7	3
	<i>Pycnopalpa bicordata</i>	6.0 ± 0.0	0.913 ± 0.056	4.4 ± 1.0	25.6 ± 2.1	8.2 ± 1.6	2
	<i>Viadana zetterstedti</i>	2.0 ± 0.0	0.634 ± 0.044	3.0 ± 0.5	15.9 ± 0.5	3.9 ± 0.7	5
Pseudophyllinae	<i>Acanthodis curvidens</i>	5.6 ± 0.6	0.305 ± 0.021	44.3 ± 10.7	12.6 ± 0.8	12.3 ± 0.5	3
	<i>Balboana tibialis</i>	6.8 ± 1.0	1.821 ± 0.217	57.2 ± 8.2	13.1 ± 1.5	7.3 ± 2.5	4
	<i>Docidocercus gigliotosi</i>	1.0 ± 0.0	0.231 ± 0.004	20.4 ± 0.4	24.2 ± 0.7	1.8 ± 0.5	5
	<i>Eubliastes pollonerae</i>	2.0 ± 0.0	0.267 ± 0.019	26.0 ± 3.5	24.5 ± 1.4	5.0 ± 1.2	5

Behavioural responses of each test bat to katydid song were scored as follows: 0 = no reaction by bat, 1 = ear movements by bat during song playback indicating song detection, 2 = change in body orientation of bat to face playback loudspeaker, 3 = bat takes flight toward or lands on playback speaker. Each bat was scored based on its highest category of behavioural interest displayed toward the playback signal. Bat responses to acoustic playback were exhibited in escalation, with higher-scoring behaviours always preceded by lower-scoring behaviours.

To determine whether each bat species had a similar level of interest in different katydid songs, we fitted cumulative link mixed models with alternative fixed effect structures using the `clmm` function in R. Bat interest score was the dependent variable, fixed effects in the models were species of bat and katydid, and the individual bat tested was a random effect. We tested all five possible model combinations, including one null intercept model. After ranking the models using the Akaike Information Criterion with a correction for small sample sizes (AICc), we determined that including both a fixed effect and an interaction component was the best-fitting full model (see Results). This shows that bat response to katydid species differed between bat species.

We then tested the data for each bat species independently to determine which katydid call parameters were relevant to the preferences of each bat species. To do this, we again used a cumulative link mixed model with the five measured call parameters (number of pulses, peak frequency, duty cycle, bandwidth and duration) as predictors, bat interest score as the dependent variable, and individual bat as a random effect. The number of pulses and duty cycle were log transformed to normalize the data distributions. Multicollinearity between predictor variables was low for each full model (variance inflation factors < 4). For each bat species, we ranked the full model with all possible combinations of predictor variables using AICc scores that were compared to Bayesian Information Criterion (BIC) scores. When the highest-ranked models for bat behaviour were nested, we tested for significant differences between the models with a likelihood ratio test. When there were no significant differences between the highest-ranked models, we selected the most parsimonious model that contained only significant variables.

(c) Echolocation call, bite force and morphological measurements on bats

For *M. microtis*, *L. silvicolum* and *T. saurophila*, echolocation calls were recorded with a condenser microphone (CM16, CMPA pre-amplifier unit; Avisoft Bioacoustics) and an UltraSoundGate 116 analogue to digital converter (500 kHz sampling rate, 16 bit resolution; Avisoft Bioacoustics). For *T. cirrhosus*, echolocation calls were recorded with a custom-made real-time recorder (480 kHz sampling rate, 16-bit resolution; PC-Tape, Animal Physiology, University of Tübingen, Germany). For each bat species, we measured three acoustic parameters of the echolocation calls: duration, peak frequency and bandwidth (same definitions as for katydid calls). These parameters are believed to be relevant to foraging in cluttered habitats [26,27]. We compiled measurements of bite force and three morphological measurements related to manoeuvrability (mass, relative wing loading, aspect ratio) from the literature (table 2).

(d) Katydid palatability to bats

We offered 15 species of wild katydids (including the 12 species we used in our acoustic playback experiments, two species with prominent defensive spines, *Steirodon careovirgulatum* and *Steirodon stalii*, and one with large mandibles, *Neoconocephalus affinis*) to *L. silvicolum* and *T. saurophila* and quantified consumption by the bats. Katydid were left overnight with bats in a small (1.42 × 2.03 × 1.27 m) tent, presented in flight to the bats in the flight cages, or held in front of the mouth of a roosting bat allowing the bat to accept or reject the prey. We tallied the number of each katydid species that was accepted and eaten completely (except for wings and legs) for each bat species.

3. Results

(a) Bat responses to katydid calls

Using AICc ranking of cumulative link mixed models based on the complete dataset with all four bat species, we first found a significant effect of bat species on responses to

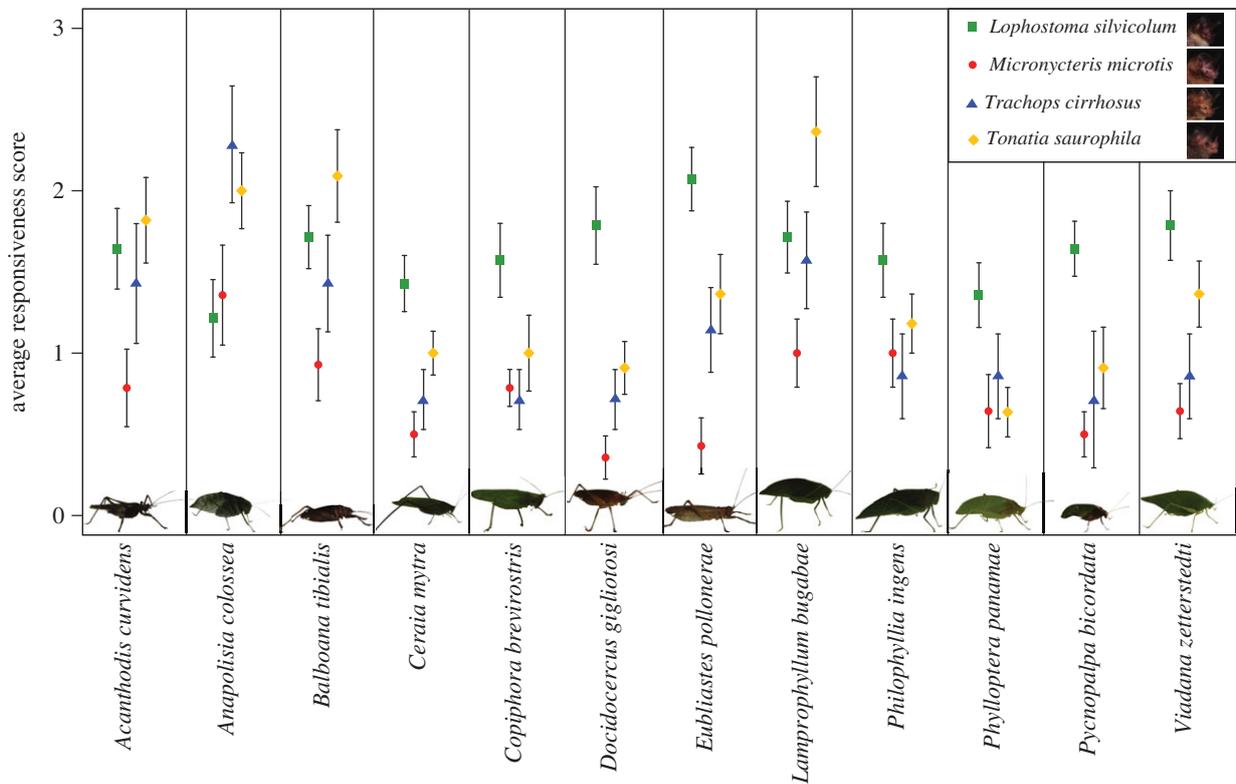


Figure 2. Response scores of four gleaning bat species to playbacks of calling song from 12 katydid species (mean \pm s.e.). Bat response scores: no reaction (0), ear movements during song playback (1), orientation to face playback speaker (2), flight towards or landing on playback speaker (3). (Online version in colour.)

Table 2. Morphological, bite force and echolocation call measurements for four Neotropical gleaning bat species. Values are means \pm s.d. (when available); sources in square brackets.

		<i>Tonatia saurophila</i>	<i>Lophostoma silvicolum</i>	<i>Trachops cirrhosus</i>	<i>Micronycteris microtis</i>
morphological measurements	mass (g)	36.8 \pm 2.0 [28]	34.3 \pm 2.2 [28]	34.9 \pm 2 [28]	5.7 [29]
	relative wing loading (unitless)	30.4 \pm 1.8 [30]	33.6 \pm 3.3 [30]	36.2 [30]	38 [22]
	aspect ratio (unitless)	5.9 \pm 0.2 [30]	5.3 \pm 0.2 [30]	5.8 [30]	5.6 [22]
bite force	maximum force (N)	16.4 \pm 5.1 [31]	18.4 \pm 5.4 [31]	13.5 \pm 5.2 [31]	8.3 \pm 6.2 [7]
echolocation call measurements	duration (ms)	1.1 \pm 0.4	1.5 \pm 0.1	1.0 \pm 0.6	0.4 \pm 0.09
	peak frequency (kHz)	71.8 \pm 22.8	66.4 \pm 2.5	78 \pm 16.4	104.8 \pm 13.3
	bandwidth (kHz, -20 dB re peak)	56–87	51–85	58–102	77–138
	<i>N</i> (no. bats, no. calls)	2, 14	5, 46	5, 43	6, 60

katydid calls (electronic supplementary material: Δ AICc: 4.7, Akaike weight $W = 0.913$; electronic supplementary material, table S1), meaning that each bat species showed a different preference pattern for the male calling song of different katydid species.

We then tested the hypothesis that the preference patterns of different bat species were based on differences in specific acoustic properties of male katydid calls (table 1). Using AICc ranking of cumulative link mixed models, we found that each bat species showed a preference for katydid calling song based on at least one acoustic feature. Preferred acoustic features differed among bat species (electronic supplementary material, tables S2–S8; figures 2 and 3): *L. silvicolum* preferred narrowband katydid calls, *T. cirrhosus* preferred

longer duration katydid calls, and *T. saurophila* preferred katydid calls that were longer in duration and lower in peak frequency. Two very different models had similar explanatory power for katydid song preference variation in *M. microtis*; one model found that longer-duration katydid calls were preferred, while the other favoured calls of lower peak frequency and larger spectral bandwidth.

(b) Other potential mechanisms of niche partitioning within the gleaning bat guild

Although slight differences were apparent, the bat species we studied generally had very similar echolocation call designs consisting of short duration (less than 2 ms), high-frequency,

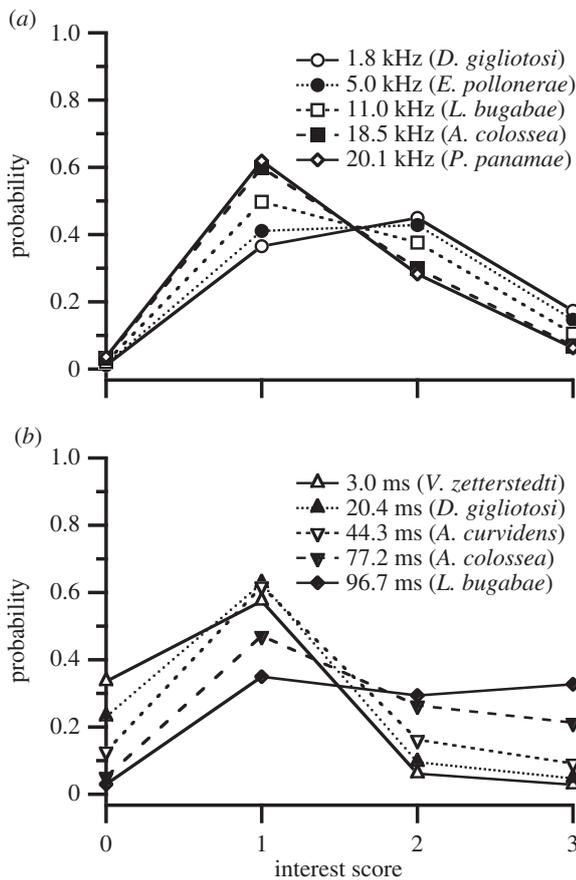


Figure 3. Probability plots for interest scores across call parameters shown to be significant in model selection of two bat species. Five katydid species are shown here for graphical clarity, but 12 species were used in the statistical analyses. The plot for *T. saurophila* is not shown because the best preference model for this species had two variables. Two models explain the best preference of *M. microtis* equally well and neither is shown. (a) Probability that *L. silvicolum* exhibited low interest-level behaviour was highest for high bandwidth calls, shifting to high probability of high interest-level behaviour for low-bandwidth calls, indicating a preference in *L. silvicolum* for low-bandwidth katydid calls. (b) Probability that *T. cirrhosus* exhibited low interest-level behaviour was highest for shorter-duration calls, shifting to high probability of high interest-level behaviour for longer-duration calls, indicating a preference in *T. cirrhosus* for longer-duration katydid calls.

broadband and multiharmonic biosonar signals (figure 4 and table 2; [32]). Bite force and morphological features relevant to prey capture were very similar across the three bat species that showed preferences for katydid call features (table 2). With the exception of *Pycnopalpa bicordata*, a small prey species that lacks spines, *L. silvicolum* and *T. saurophila* readily consumed all of the 15 katydid species offered, including katydids with numerous large spines and powerful mandibles (electronic supplementary material, table S9). Therefore, individuals of both these bat species were easily able to overcome the physical defences of their katydid prey, and there was no evidence that these bats found any of the katydids unpalatable. Both *M. microtis* and *T. cirrhosus*, the other two bat species we tested for katydid call preferences, have been previously documented to prey on large-bodied, heavily defended insects ([6]; R. A. Page 2005, unpublished data).

4. Discussion

In this study, we investigated the responses of four Neotropical substrate-gleaning bat species to acoustic playbacks of calls

from 12 katydid species and found substantial divergence among predators in their acoustic preferences for prey-generated sounds. Because predation events progress from detection and classification, through to localization, attack and consumption [21], there is potential for niche partitioning based on sensory, morphological or behavioural differences among predators at any stage in the sequence. We did not find evidence of differences in echolocation call design, morphological variables related to flight, bite force or prey-handling ability between the four bat species. Our results indicate that niche partitioning by Neotropical gleaning bats occurs early in this predation sequence and is related to species differences in sensory preferences (biases) for prey-generated sounds. This demonstrates that sympatric Neotropical substrate-gleaning bats do not impose a uniform predatory selection pressure on katydid prey signal structure. Moreover, the divergence in prey signalling preferences also reveals sensory-based niche partitioning between predatory bats.

Most, but not all, of the results conformed to our prediction of greater responsiveness by bat predators for prey signals that are more easily detected or located, such as a preference for lower-frequency calls by *T. saurophila* and longer-duration calls by *T. cirrhosus* and *T. saurophila*, and our findings are consistent with other studies reporting that eavesdropping predators prefer more localizable prey signals [33,34]. By contrast, the preference of *L. silvicolum* for narrowband katydid calls was unexpected. In general, it has been suggested that narrowband signals have evolved to impede localization by predators because they provide less information [5,35,36]. *M. microtis* lacked a clearly superior preference model for katydid acoustic signals. Although *M. microtis* might use passive hearing to detect and localize singing katydids, this species also uses echolocation to detect silent, stationary prey resting on surfaces [37]. This specialized form of prey detection may explain the preference for model ambiguity. Indeed, of the four gleaners we studied, *M. microtis* was the least responsive to katydid calls (figure 2), and their echolocation calls were also the least similar to the three other bat species (figure 4, table 2), indicating that this species may be employing a complex foraging strategy. The differences in responsiveness to katydid calls between the four bat species might also reflect differences in their peripheral (e.g. audiograms) or central auditory processing.

Our results indicate that subtle differences in prey selection are occurring in this gleaning bat guild, with differences in sensory preferences for prey signals being the underlying mechanism responsible for the divergence. Therefore, eavesdropping by predatory substrate-gleaning bats cannot serve as a generalized selection pressure resulting in similar changes to the acoustic features of male katydid call structure. Likewise, no single type of generalized male katydid call structure can provide protection against all types of eavesdropping gleaning bats.

Lophostoma silvicolum has been previously shown to prefer katydid species with high duty cycles to species that call sporadically [5], and it has been hypothesized that katydids evolved low-bandwidth and high-frequency calls in response to bat predation [36]. Some katydids that call in habitats where gleaning bats forage have been shown to produce low duty cycle calls [5]. Despite these findings, katydids that live in the presence of gleaning bats defy expectations with diverse and sometimes highly conspicuous calls. Non-uniform predatory selection pressure on the parameters of prey-generated sounds may contribute to, or maintain,

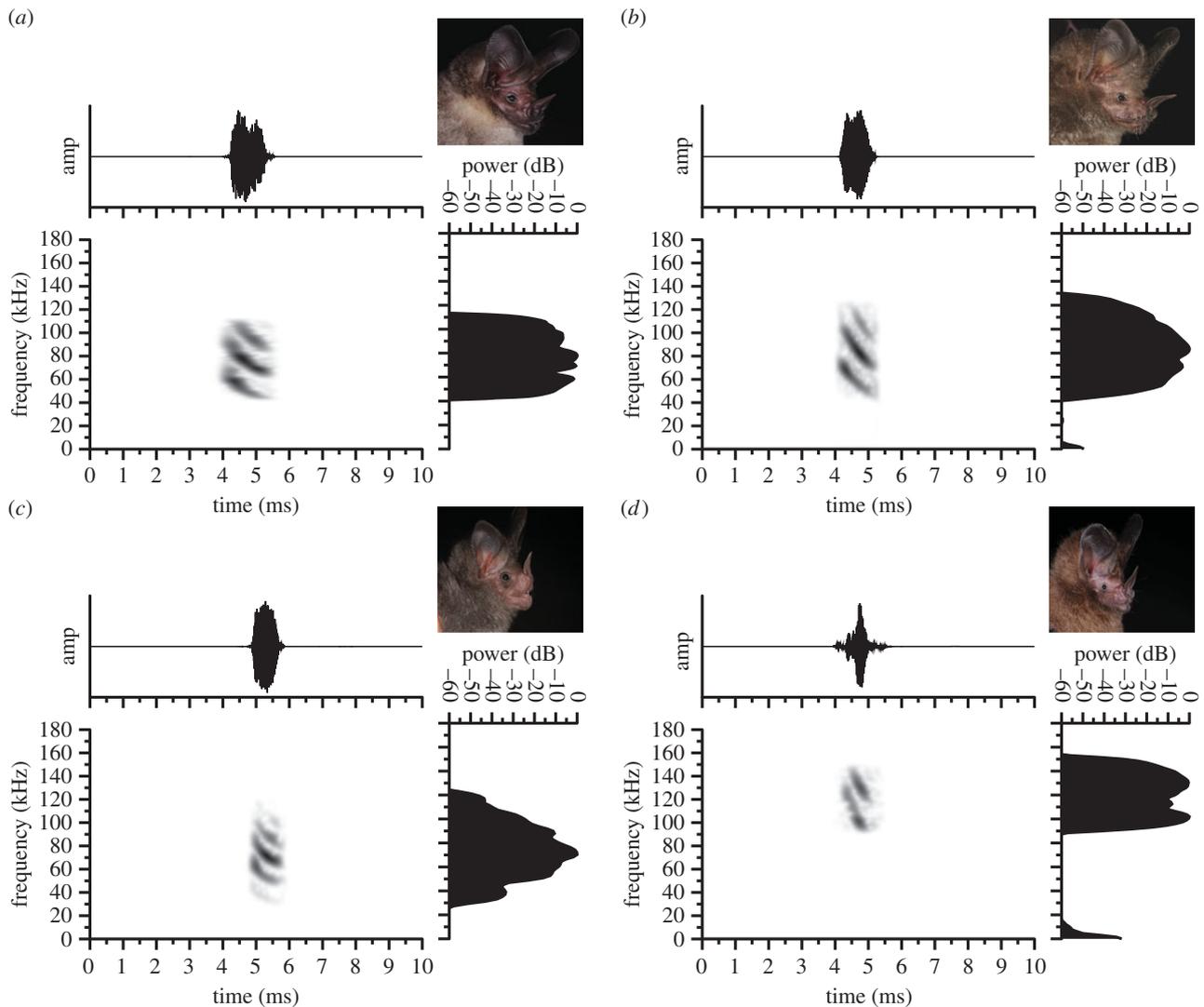


Figure 4. Echolocation calls of four species of Neotropical substrate-gleaning bats. Search phase echolocation calls of the (a) white-throated round-eared bat *Lophostoma silvicolum*, (b) fringe-lipped bat *Trachops cirrhosus*, (c) stripe-headed round-eared bat *Tonatia saurophila* and (d) common big-eared bat *Micronycteris microtis*. Top trace: oscillogram; bottom left trace: spectrogram; bottom right trace: power spectrum. (Online version in colour.)

signal diversity in at least two ways. First, if no single call structure provides protection against all eavesdropping predators, then there may be reduced selection to evolve signals that are less preferred by predators. In this case, the effects of sexual selection (mate signalling) could outweigh those of natural selection (predator evasion), resulting in the evolution of communication signals that are easily recognized and preferred by females, rather than ones that minimize predation risk [38–40]. Alternatively, predation pressure could select for signal diversity when predators with different preferences vary in their spatial distributions. In the latter scenario, differences in signal structure can be expected to evolve in response to the predation pressures specific to a particular microhabitat. Although the geographical ranges of the four gleaning bat species we studied overlap, how gleaning bat predators distribute themselves across microhabitats is not well understood. Kalko *et al.* [41] tracked the movements of two *T. cirrhosus* and three *L. silvicolum* on Barro Colorado Island in Panama, and found that the individual foraging areas of each species did not overlap. Another Barro Colorado Island tracking study [42] found that *T. saurophila* foraged in areas overlapping with the home ranges for *T. cirrhosus* and *L. silvicolum* from Kalko *et al.* [41]. In our study, we occasionally captured

two (and rarely three) of our four focal bat species in the same mistnet, demonstrating that, at times, these species have overlapping foraging and commuting areas.

Niche partitioning at a fine scale plays an important role in species diversity in tropical regions [43]. Sensory variation among animals that coexist within a community is an understudied, but potentially important, partitioning mechanism that may go undetected without detailed studies of behaviour [15]. Niche partitioning typically increases resource use [44] and causes stabilizing selection pressure [45]. Experimentally, it has been shown that the predatory influence of substrate-gleaning bats is a critical component of Neotropical insect control, and in turn, plant productivity [46,47], demonstrating the significant exploitation of insects as a prey resource. Sensory niche partitioning probably contributes to the coexistence of high numbers of substrate-gleaning species in Neotropical bat communities.

We have demonstrated that predator response varies substantially even within a single family of insect prey, indicating that the evolution of specialized predator–prey behaviours may be occurring at a more narrow scale than previously detected [1,8]. Using discarded or digested remains of insects has historically limited dietary studies in insectivores to prey identification at the level of order or family [28,48,49], and the description of many insectivorous bats as prey generalists

with overlapping diets may actually be an artefact of this type of broad identification [20,50,51]. Behavioural observations coupled with modern techniques of prey identification, such as DNA barcoding, will be essential for clarifying the degree of niche partitioning in ecologically similar species [52].

5. Conclusion

Sensory-based variation between multiple predator species has the potential to play an important role in prey signal evolution and diversity. By testing for behavioural differences between predators, we can expose cryptic differences in foraging niches and prey preferences. To fully understand the relationship between within-guild predator variation and the evolution of prey signals, a more detailed understanding of prey–predator distributions and predator diets is needed. We conclude that multiple predators that have diverged through sensory-based niche partitioning may play an important role in specialization between ecologically similar species, and that variations in predator specializations probably play a role in the evolution of prey communication signals.

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