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The ontogeny of decision-making in an eavesdropping predator

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Predators use prey-emitted cues to assess and localize potential food sources. Sexual advertisement calls offer conspicuous cues for eavesdropping predators. While the ontogeny of predatory behaviour is key for survival and can determine adult responses, our understanding of the development of the responses to prey-emitted cues is limited. Here, we measured the responses of juvenile and adult fringe-lipped bats (*Trachops cirrhosus*) to the acoustic advertisement calls of co-occurring anurans. We confirmed that adult bats modulate their foraging behaviour based on their prey's acoustic cues associated with prey palatability. The responses of juvenile bats revealed that ontogeny plays an important role in bat predatory responses. In contrast to adults, prey palatability did not predict predatory behaviour in juveniles, which responded strongly to poisonous toads and little to some palatable frog species, suggesting that avoidance of poisonous species is learned through experience. Despite these differences, both juveniles and adults appeared to attend to acoustic cues related to body size. Our results support the hypothesis that, over development, acoustic preferences of eavesdropping predators become more closely aligned with advantageous foraging outcomes. Overall, these results offer the first evidence of developmental changes refining decision-making in an eavesdropping predator in the wild.

1. Introduction

Classic examples of predator learning involve traits such as aposematism, where predators learn to recognize often-reliable warning signals of unpalatability [1–4]. Eavesdropping predators, however, must rely on cues that are not intended for them. Such predators capitalize on conspicuous traits of prey which often emerge through sexual selection, such as highly visible and contrasting colours, rich and intense chemical lures or loud and continuous vocalizations [5–7]. Predators thus face the challenge of navigating the often complex landscape of prey-emitted signals and establishing associations between prey-emitted cues and their various outcomes to determine their foraging responses. This challenge is especially true for generalist eavesdroppers, which are less likely to have tight evolutionary associations with their prey or to have highly specialized sensory adaptations that enhance their detection of target species signals, compared to specialist eavesdroppers [7].

Predator associations between prey cues and prey quality can be fixed or can vary across time. Examples of fixed associations include juveniles of

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two Neotropical avian predator species (turquoise-browed motmots [8] and great kiskadees [9]) which show an innate aversion to coral snake colour patterns. Similarly, newborn garter snakes demonstrate innate responses to prey chemosensory cues that generally coincide with the local population's diet, suggesting a genetic basis for these responses [10,11]. In contrast to these fixed associations within individual predators, spatially and temporally variable environments may select for plastic associations.

Learning, both social and individual, can mediate associations between prey cues and prey quality, as many predators form such associations through their experience with prey and through the observation of others [12,13]. For example, learned associations can be rapidly instilled by a formative experience, such as a noxious taste or extreme illness following ingestion of unpalatable prey (e.g. jays and butterflies [14], bats and tiger moths [15]). Social learning can occur through the observation of others making foraging decisions, or through explicit demonstration, and is especially common among relatives, such as offspring observing their parents [16,17]. Learning could be especially important for generalist eavesdropper species that must sort the cues of many potentially palatable and unpalatable prey.

The fringe-lipped bat (*Trachops cirrhosus*) offers an excellent system to understand how predators use cues from prey to make foraging decisions, and how these processes change during development. Adult *T. cirrhosus* are generalist eavesdroppers on frogs and use the frog's call to distinguish palatable from unpalatable prey, informing their decision whether or not to attack [18–22]. The fact that *T. cirrhosus* can rapidly learn to respond to novel acoustic cues with foraging behaviours that can last for years [23–25] leads us to hypothesize that learning plays an important role in shaping their acoustic eavesdropping responses over development. However, little is known about the ontogeny of these foraging behaviours nor the specific acoustic features that individuals use during decision-making.

Here, we tested the responses of adult and juvenile individual *T. cirrhosus* to acoustic playbacks of the mating calls of 15 sympatric anuran (frog and toad) species to understand how predator responses change with development. These species included anurans known to be palatable, toxic or too large to handle (electronic supplementary material, table S1). To better understand the information used to assess their prey, we also analysed potential acoustic features that could predict the behaviours of both juvenile and adult bats.

2. Methods

(a) Animals

Trachops cirrhosus were captured along streams using mist nets in Soberanía National Park, Panama, and tested in phonotaxis experiments (figure 1A). Juveniles were identified by the presence of epiphyseal gaps in the phalanges [26]. Twenty adults (n = 5♀/15♂) were captured and tested between 2007 and 2008 and 19 juveniles (n = 9♀/10♂) were captured and tested between 2010 and 2012. One additional adult (♀) was captured and tested in 2011. Capture records of *T. cirrhosus* indicate that this population gives birth around the time of the transition from dry to wet season (April–June) [27], with young fledging and foraging independently between June and September (figure 1B). We caught and tested juveniles in June and July; thus, these individuals were likely to have had some experience foraging for frogs that call during the wet season (May–December), but limited experience with frog species that call primarily during the dry season (January–April). Adults were tested in January–March or June–August.

Following testing, all bats were marked with a subcutaneous passive integrated transponder (PIT) tag (Biomark, Boise, ID) and released at the site of capture.

(b) Prey types

To investigate the responses of the bats to diverse acoustic signals from species that vary in size and palatability, we tested bats on calls from 15 anuran species from five families that are common in the area: three Leptodactylidae (foam-nesting frogs), eight Hylidae (tree frogs), one Eleutherodactylidae (direct developing rain frogs), one Centrolenidae (glass frogs) and two Bufonidae (true toads) (figure 1C). We classified prey into two categories based on evidence of palatability (figure 1C; see electronic supplementary material, table S1 for details on how palatability was assessed). We define palatable prey as those that the predator is able to consume, and unpalatable as those that cannot be consumed due to their large size and/or the presence of toxins. Four species were considered unpalatable: two species that produce bufotoxins (*Rhinella alata* and *R. marina*) [28]; one species too large to consume, with some chemical defences, and an opportunistic predator of bats (*Leptodactylus savagei*) [29–31]; and one other species too large to consume (*Boana rosenbergi*). The remaining frogs were classified as palatable based on observations during palatability tests (see electronic supplementary material, table S1), past flight cage experiments [22,32–35], faecal DNA barcoding results [36], and knowledge of their body size and lack of known toxins. Given that the experience of *T. cirrhosus* with different prey is expected to be correlated with frog seasonal activity, we also categorized prey by their seasonal availability [37], with particular interest in species that call primarily during the dry season (*Smilisca sila*, *R. alata* and *R. marina*; figure 1C). Data on body size (snout–vent length in mm; SVL) were obtained from [37].

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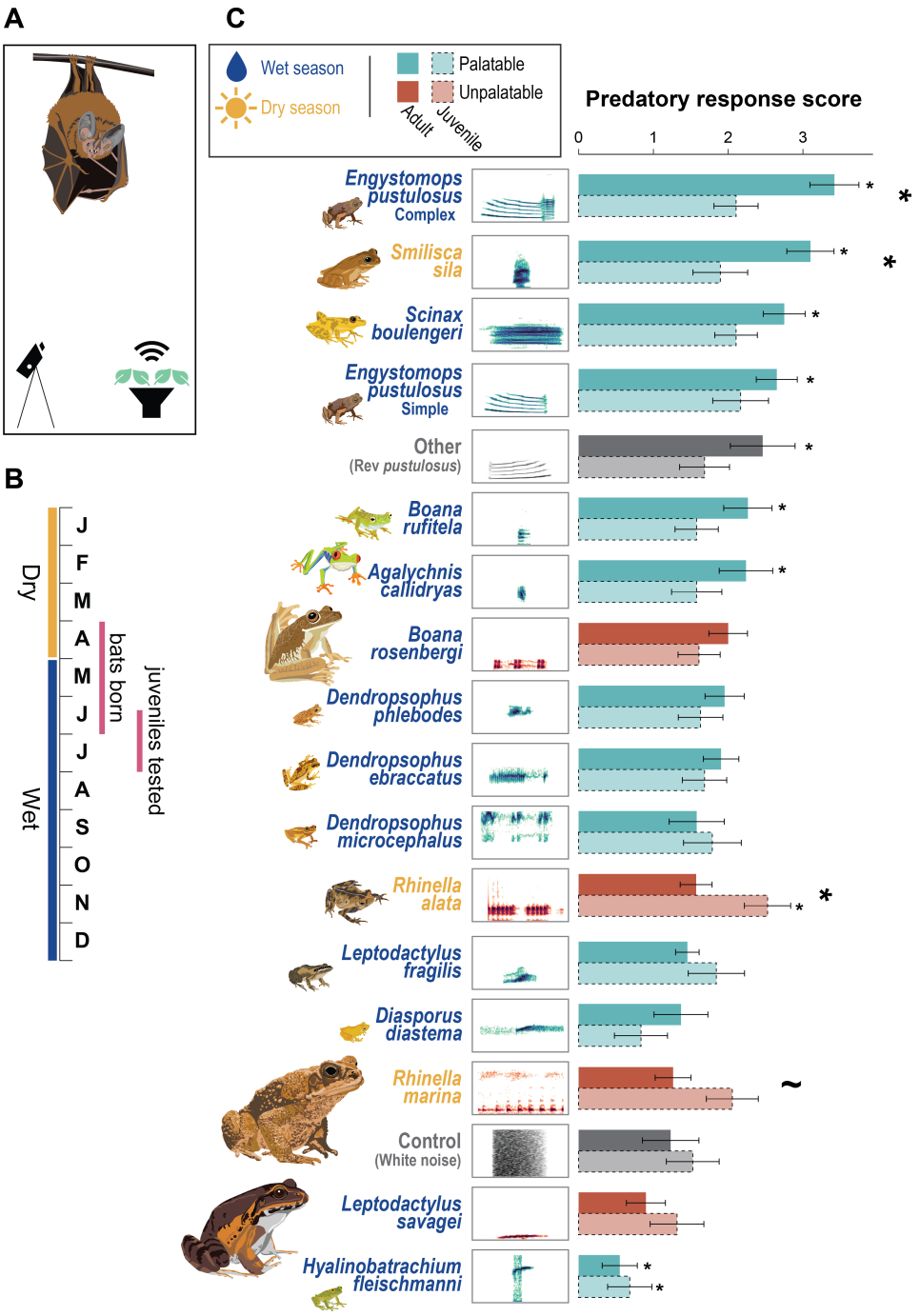

Figure 1. (A) Experimental setup, with the speaker and camera not to scale, illustrating the approach to examine the predatory response of frog-eating bats (*Trachops cirrhosus*). (B) Timeline of seasons in Panama and when the experiments were performed with juvenile bats relative to when they were born. (C) Predatory responses of juvenile and adult bats to the advertisement calls of anurans in this community. The colour of the species name indicates the primary season in which they call in this area (yellow = dry season, blue = wet season). Sample spectrograms of the call from each species, as well as two synthetic stimuli (grey), illustrate the diverse acoustic stimuli used. Each spectrogram is 0.5 s in duration (*x*-axis) and spans from 0 to 7 kHz (*y*-axis), with darkness indicating amplitude. The bars depict the predatory response scores (mean ± s.e.) from adult (solid) and juvenile (lighter with dashed borders) bats. The colour of the bar indicates our assumed measure of palatability (teal = able to be consumed, red = unable to be consumed), for more detail, see electronic supplementary material, table S1. Small asterisks above a single bar indicate significant ($p < 0.05$) differences from the white noise stimuli within each age category. Larger asterisks between bars indicate stimuli for which we observed a significant effect of age ($p < 0.05$), and the tilde indicates a non-significant trend for an effect of age ($p < 0.07$) when comparing the response of adults to the responses of juveniles for a particular acoustic stimulus. The panels are sorted based on responses of adults from top (more) to bottom (less). Illustrations by Damond Kyllo.

(c) Acoustic stimuli

The advertisement calls of 5–10 individuals from each species were recorded from frogs local to the test site. The recordings were acquired during a large survey of the area by a variety of individual researchers (see Acknowledgements). Recent recordings were made with a Sennheiser ME64 microphone and a Marantz PMD-661 recorder; older recordings were made with a Nagra reel-to-reel tape recorder.

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We tested the behavioural response of each bat in standard playback experiments [38], using up to 18 acoustic stimuli. All stimuli were standardized to play at the same peak amplitude (75 dB sound pressure level re. 20 µPa at a distance of 1 m from the speaker) with 1.5 s of silence between each call. We also tested 10 adult bats (5 from the main experiment and 5 novel bats) using the same stimuli but with call rates matching the natural species' call rates to ensure that the standard duration of silence between each call did not influence the bats' behaviour (electronic supplementary material, figure S1).

For our acoustic analyses of calls, we measured 13 call parameters. Five of these were (1) call duration, (2) call rise time (time from the beginning of the call to the time reaching peak amplitude), (3) peak frequency, (4) initial peak frequency (peak frequency during the first 5 ms of the call) and (5) final peak frequency (peak frequency during the final 5 ms of the call). For calls with more than one note, we also measured (6) the number of notes per call, (7) note duration, (8) note rise time and (9) note shape (unitless variable derived by dividing the note rise time by note duration). Finally, if notes had more than one pulse, we measured (10) the number of pulses per note, (11) pulse duration, (12) pulse rise time and (13) pulse shape. If a call had more than 15 notes, and if any note had more than 15 pulses, we measured features for the first 5, middle 5 and final 5 notes and/or pulses. For a diagram depicting the call segmentation, see electronic supplementary material, figure S2. All features were measured using Raven 1.3 (ravensoundsoftware.com).

(d) Acoustic playbacks and predatory response scores

To assess the responses of the bats to frog calls, phonotaxis experiments were conducted between 1830 h and 0300 h in a 5 × 5 × 2.5 m flight cage under ambient levels of humidity and light, with additional illumination by a 25W red light bulb and Sony HVL-IRM infrared lights. All trials were recorded with a Sony Handycam DCR-SR45 digital video camera set on NightShot mode.

We placed one Fostex FE103En speaker underneath a 1.5 × 1.5 m screen that was covered in leaf litter in one corner of the flight cage. Stimuli were broadcast from a Dell Latitude E4300 computer using a SA-150 Realistic amplifier at an amplitude of 75 dB SPL (re. 20 µP) measured at 1 m from the speaker using an SPL meter (Radioshack). If the bat left the roost, the next trial began after the bat returned to the roost.

Observers unaware of the hypothesis scored the videos of bat responses by assigning a numeric value to each trial, reflecting the bat's level of interest in the stimulus. From our experience with these bats [39,40], a typical predation sequence begins with the bat hanging quietly from a perch; when the bat hears the frog call, it turns its head and ears rapidly, orienting towards the sound source. The bat may then flex its wings, fly towards the frog call and land on its prey (electronic supplementary material, video S1). We scored behaviours on a 0–5 point scale of increasing predatory interest in the stimulus: no reaction (0), slight ear motions (1), vigorous ear motions (2), wing flexes (3), flight towards the speaker (4) and landing on or attacking the screen covering the speaker (5).

We created ten sets of calls, and the set number and order of calls presented was randomized for each individual bat. The trials were 30 s in length and were presented at five-minute intervals. However, for the first adult bat, trials were terminated after 10 s. After testing eight adult bats, we obtained recordings from one additional frog species (*L. labialis*), and we added two artificial stimuli to test for responses to novel sounds: a túngara call played backwards ('*rev. pustulosus*', an acoustic stimulus that has the frequency but not the temporal components of a call *T. cirrhosus* strongly prefers) and a white noise burst. All subsequent bats were tested with this full suite of acoustic stimuli (figure 1C), except two adult individuals who, because of testing difficulties, were only tested on a subset of the stimuli (7 and 12 calls, respectively).

(e) Statistics

Behavioural responses were analysed independently for juveniles and adults using linear mixed-effects models in R (package: *lme4*), with the response as the dependent variable, stimulus as the independent variable, and BatID as a random effect to account for repeated responses from each bat. To compare adult and juvenile bats, we also included age class (adult or juvenile) as a fixed effect in a full factorial model with stimulus as the other fixed effect. For our analyses with acoustic features, linear regressions of mean bat response were run against each call parameter individually as well as in aggregate using principal components analysis (with data first transformed to *z*-scores). Data for all acoustic features were log-transformed to improve normality except for note shape and pulse shape. *F*- and *p*-values were calculated using Type II ANOVA with Satterthwaite's method (package: *lmerTest*). Post-hoc pairwise comparisons were conducted using Tukey's tests (package: *emmeans*).

3. Results

(a) Acoustic preferences of adult bats

We tested the responses of adult bats (n = 21) to 18 acoustic stimuli and found that the stimulus affected their predatory responses ($F_{17,300}$ = 9.7, p < 0.0001; figure 1C). With the white noise playback set as a baseline control, we observed stronger responses to *E. pustulosus* (complex, simple and reversed; see §2), *S. sila*, *S. boulengeri*, *B. rufitela* and *A. callidryas*, as well as weaker responses to *H. fleischmanni*. After pooling the responses by prey palatability, we found that adult bats responded more strongly to palatable than unpalatable prey (score: $F_{1,290}$ = 17.6, p < 0.0001; figure 2A).

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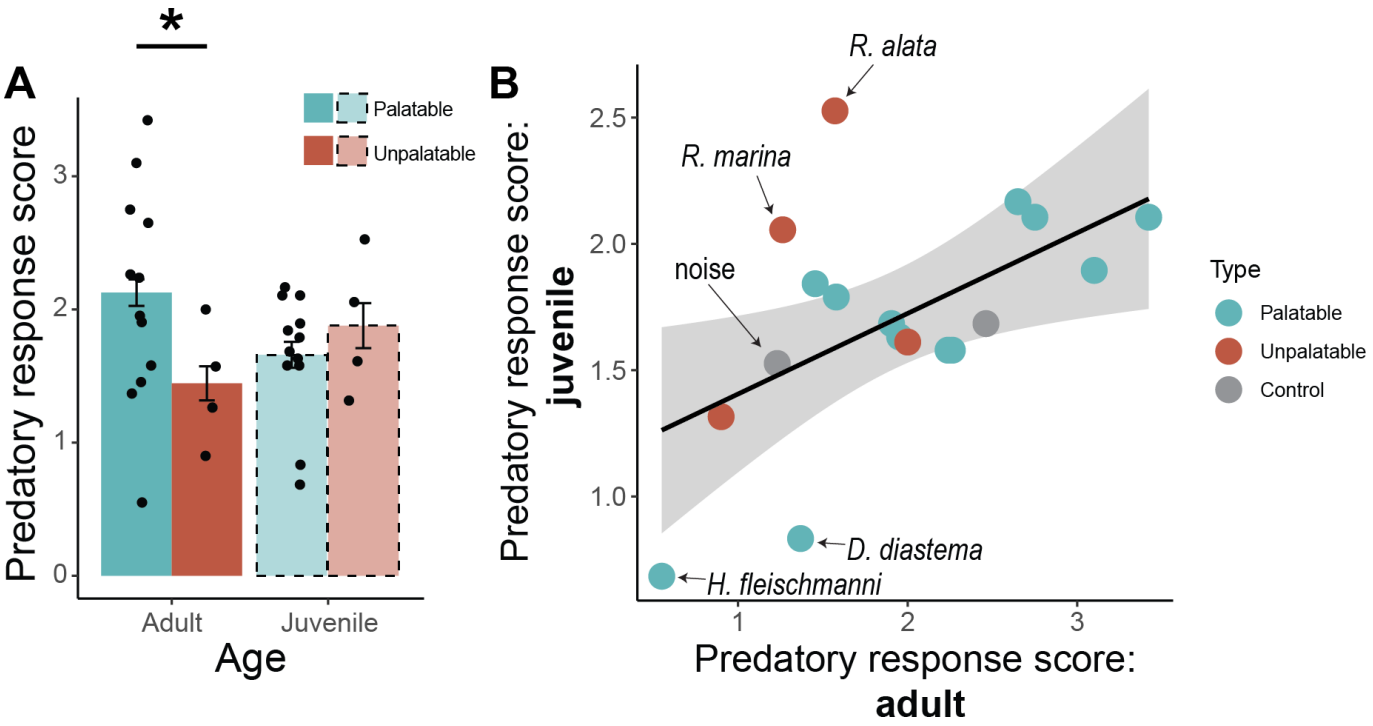

Figure 2. (A) Predatory response scores pooled across frog species by prey palatability, with bars indicating the mean ± s.e. The asterisk indicates a significant difference within adults between palatable and unpalatable prey ($p < 0.05$). (B) Correlation between mean behavioural responses of adults and juveniles for each stimulus.

(b) Developmental shifts in acoustic preferences

To understand how responses to prey stimuli change across development, we tested juvenile bats ($n = 19$). As with adults, the stimulus affected bat responses ($F_{17,302} = 2.7$, $p = 0.0003$; figure 1C). With the white noise playback set as the baseline control, we observed stronger responses to a non-palatable species (*R. alata*) and weaker responses to a palatable one (*H. fleischmanni*). After pooling the data by prey palatability, we saw no significant difference for juvenile responses to palatable and unpalatable prey ($F_{2,280} = 2.0$, $p = 0.1575$; figure 2A).

To test the effect of age on predatory responses, we analysed the data from all bats together. Responses to the acoustic stimuli differed based on the age class of the bats, as identified by the interaction between age (juvenile vs adult) and stimulus ($F_{17,602} = 3.1$, $p < 0.0001$). Given this interaction, we tested for an effect of age class on the response to the call of each prey species independently. We found that adult bats responded more strongly than juveniles to two palatable species: *E. pustulosus* (complex) and *S. sila* ($p < 0.02$ for both). Juveniles responded more strongly than adults to a non-palatable species, *R. alata* ($p = 0.0138$), and marginally non-significantly more strongly to another non-palatable toad, *R. marina* ($p = 0.0665$). Despite these differences in response, we observed a positive correlation between the mean response to each stimulus for each age class ($F_{1,16} = 6.7$, $p = 0.0195$; figure 2B). Finally, we pooled the dataset within prey-type category and observed a significant interaction between age class and prey type ($F_{1,570} = 15.6$, $p < 0.0001$). The only significant *post-hoc* contrast was between palatable and unpalatable prey in adult bats (Tukey's test: $p = 0.0002$; figure 2A).

(c) Acoustic correlates of call responses

We examined whether acoustic features predict (1) prey palatability and (2) bat predatory behaviour. If any acoustic cues are reliably associated with unpalatable and palatable prey, we hypothesized that adult bats could use those cues to modulate their responses. We thus asked if the acoustic features we measured predict prey palatability. Indeed, five features varied with palatability (call duration: $F_{1,14} = 6.1$, $p = 0.0272$, call rise time: $F_{1,14} = 6.2$, $p = 0.0262$; peak frequency: $F_{1,14} = 8.1$, $p = 0.0128$; initial peak frequency: $F_{1,14} = 12.9$, $p = 0.0030$; final peak frequency: $F_{1,14} = 12.9$, $p = 0.0030$; electronic supplementary material, figure S3). Unpalatable frogs tended to have longer call durations and call rise times along with lower peak frequencies.

To examine the joint effect of multiple acoustic features, we aggregated the call features using principal components analysis (PCA). The first three PCs explained 38%, 20% and 19% of the variation, respectively (figure 3A). All five features that predicted prey palatability loaded heavily on PC1, with call duration and call rise time having positive coefficients, and all three peak frequency measures having negative coefficients (electronic supplementary material, table S2). Relatedly, PC1 also varied by prey palatability ($F_{1,14} = 11.1$, $p = 0.0050$; figure 3B). We did not observe clustering of prey types in PC2 or PC3.

Because large frogs cannot be handled by the bats and are thus considered unpalatable (figure 1C) and peak frequency measures load negatively on PC1, it is unsurprising that PC1 also correlates positively with body size ($F_{1,14} = 16.6$, $p = 0.0011$; figure 3C). Thus, these analyses indicate that the acoustic features that most separate the call stimuli also provide information on body size and, relatedly, palatability.

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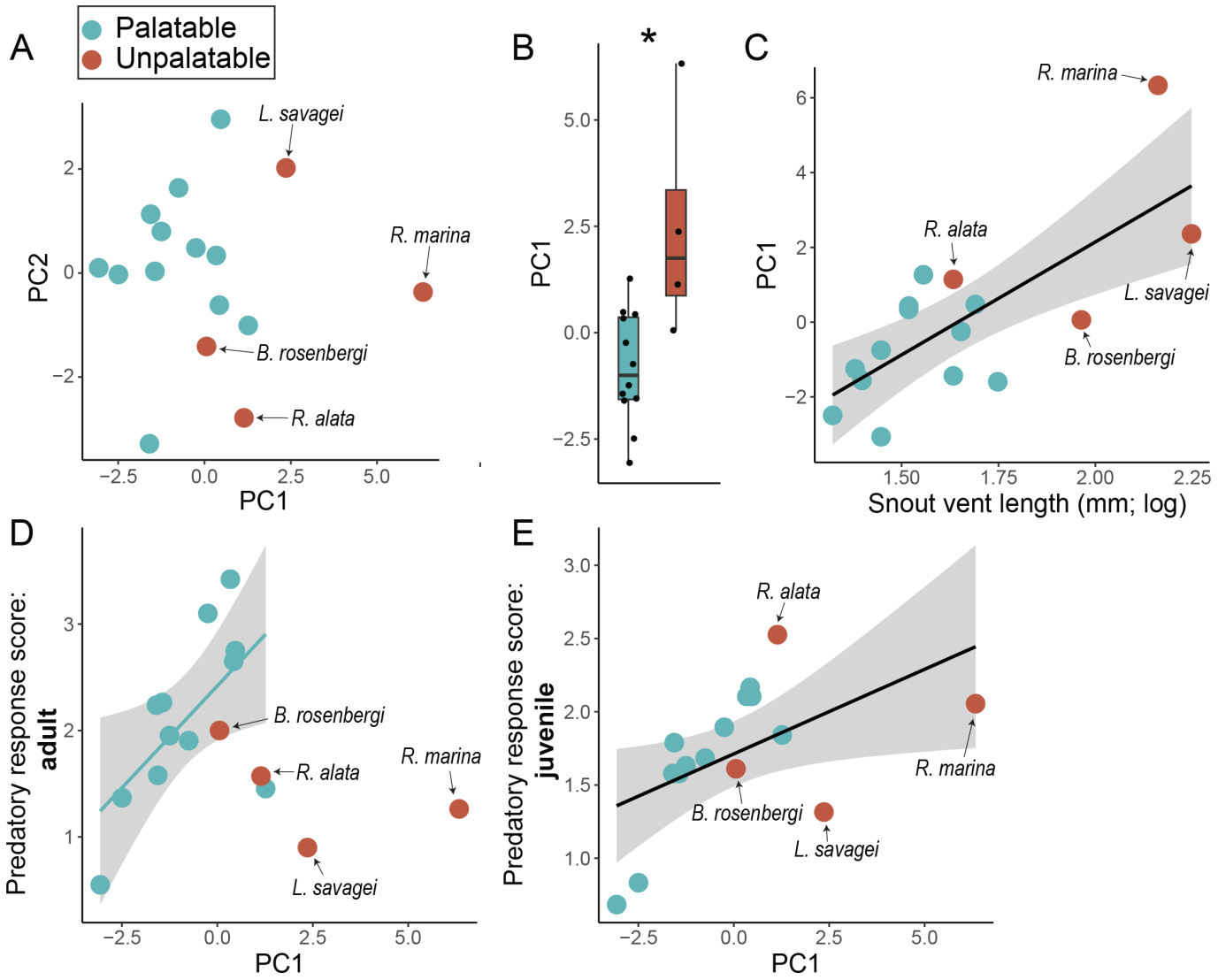

Figure 3. Acoustic properties of frog calls, palatability and responses of juvenile and adult bats. (A) Clustering of frog call species based on PC1 and PC2. (B) PC1 significantly differs by prey palatability. (C) Body size and PC1 are significantly correlated. (D,E) Correlations between PC1 and the behavioural scores of adults (D) and juveniles (E). In (D), the trendline is limited to palatable species, while in (E), the trendline depicts the overall relationship across all species.

Given that PC1 predicts prey palatability, we investigated whether this composite measure of acoustic features predicts the responses of adult and/or juvenile bats. For adult bats, we observed no significant correlation between PC1 and their responses ($F_{1,14}$ = 0.0, p = 0.8270). However, when we included the interaction between PC1 and prey palatability as a predictor of behaviour, we observed a significant interaction ($F_{1,11.0}$ = 4.9, p = 0.0470) which was driven by a strong relationship between PC1 and behavioural score for palatable species (which was significant when analysed separately: $F_{1,10}$ = 6.3, p = 0.0315; figure 3D). For juvenile bats, we observed a positive relationship between PC1 and predatory response scores across all species ($F_{1,14}$ = 5.8, p = 0.0310; figure 3E). We observed, however, no significant interaction between PC1 and palatability on the predatory response score ($F_{1,12}$ = 0.9, p = 0.3621).

4. Discussion

In this study, we measured the predatory responses of adult and juvenile fringe-lipped bats (*Trachops cirrhosus*) to the mating calls of 15 of the most common sympatric frog and toad species in Soberanía National Park, Panama. Confirming previous results in this species, and in other eavesdropping bats, we found that the responses of adult bats varied according to prey species [41,42], and were significantly predicted by the palatability of the prey species [18,19,22]. While juvenile bats also significantly varied in their responses to the calls of different species, in contrast to the adults, prey palatability did not predict their responses. Indeed, juvenile bats showed strong predatory responses to the calls of highly unpalatable species (the poisonous toads *R. alata* and *R. marina*), calls that were ignored by older, more experienced bats. In contrast, juveniles showed low predatory responses to some of the adults' preferred and highly palatable prey species, specifically complex calls of the túngara frog, *Engystomops pustulosus*, and calls of the dry season calling tree frog, *S. sila*. Our results provide the first evidence for the hypothesis that the preferences of eavesdropping predators change across development, becoming more closely aligned with advantageous decision-making over time.

Despite the finding that juvenile and adult bats differed in their responses to some stimuli, we observed that their overall responses were significantly correlated, which may arise from similarities in responses to specific acoustic features. Our acoustic

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analyses indicated that the call properties best separating the stimuli (i.e. longer and lower frequency calls loading most heavily on PC1) also correlated strongly with prey body size and differed based on palatability (with larger frogs generally being unpalatable). This relationship reveals the subtle interaction between prey energy and handling that ultimately mediate prey profitability because, while the largest species are best avoided by the bat, within palatable prey, larger species should provide a more valuable foraging opportunity. Consistent with this prediction, adult behaviour correlated positively with PC1, but only for palatable prey. In contrast, juvenile responses correlated positively with PC1 more generally. Thus, it appears that juveniles have early biases to attend to acoustic features that predict body size but require experience to learn that the largest species are not palatable.

Given the typical timing of breeding in this bat [27], the juveniles we tested are expected to have had the least experience with anuran species that call primarily during the dry season. Indeed, we observed significant differences between adult and juvenile responses for the palatable species that is most active in the dry season (*S. sila*), the only tree frog species for which we observed significant age-dependent responses. Furthermore, the two unpalatable toad species (*R. marina* and *R. alata*) call primarily during the dry season, and juveniles tended to respond to the calls from these species more strongly than adults. Together, these data suggest that direct experience with calling frogs shapes subsequent behaviour, with efficacy of bat foraging decision-making improving with time.

The combination of the wide geographic range of frog-eating bats [43] and the small foraging area of individuals (approx. 12 ha [39,40]) probably heightens the importance of learning as a mechanism in predatory decision-making. Across their species ranges, frog-eating bats encounter a wide range of potential prey. But each individual bat encounters a much smaller subset of prey and probably learns to respond appropriately to these specific local prey species over time. Indeed, evidence from both this and previous studies suggests that acoustic responses in this species are shaped by the local anuran community. In this study, adults responded more strongly than juveniles to the complex (but not simple) calls of the túngara frog (*E. pustulosus*), a particularly abundant frog in the study area. In contrast, in *T. coffini*, a closely related species (formerly subspecies), tested in an area of Costa Rica without túngara frogs, individuals do not respond more strongly to complex calls [18] (but see the response of *T. cirrhosus* in Ecuador to complex calls of another frog species [44]). The preference of adult *T. cirrhosus* for complex calls does not appear to result from perceptual biases [45], suggesting that bats learn and remember particular prey cues. In the case of the complex túngara frog calls, for instance, they may be associating the added component of the call (the 'chuck') with higher prey density [46]. Interestingly, the adult and juvenile bats in this study were equally responsive to the reversed túngara call and the simple call, indicating that responses are permissive to this temporal aspect of acoustic variation. This finding is consistent with previous experiments showing that these bats are more permissive in their responses to túngara frog calls than female frogs are [47].

The risks and benefits associated with attacking different frog species vary along a continuum. For example, within palatable prey, larger species often offer a greater caloric reward. Our results suggest that bats attend to this variation, responding more strongly to larger species of palatable prey. Within unpalatable species, two species examined here (*R. alata* and *R. marina*) produce toxic bufotoxins [28]. However, experiments in which *T. cirrhosus* attack normally non-toxic prey that are covered with *Rhinella* bufotoxins show that bats can quickly detect the toxin and eject the prey, suffering no long-standing negative consequences [33]. This ability to quickly assess toad toxicity may explain why responses to these two unpalatable species were not as low as responses to *L. savagei*. Not only is *L. savagei* chemically defended [30], but it is also an opportunistic predator of bats, including those as large as *T. cirrhosus* [29]. Additionally, the largest responses towards an unpalatable species were to *B. rosenbergi*. While this frog is generally too large for bats to handle, we have observed bats consuming *B. rosenbergi* when the frog was already euthanized (see electronic supplementary material). Altogether, our results suggest that bats attend to the variation in prey quality within the broader palatable and unpalatable categories.

Individual physiological changes, within prey or predator, can also temporally modulate prey palatability. For example, while we classified the red-eyed tree frog (*A. callidryas*) as palatable given observations of bats consuming them in palatability tests (see electronic supplementary material), this frog species is known to secrete a variety of chemicals that may function to deter predators [48]. We observed that when agitated, males of this species release an odour, at which point captive bats would refuse to consume them, suggesting that bats may deem this species unpalatable in certain conditions. On the predator side, *T. cirrhosus* has unusual structures in the submandibular salivary glands, which "could be the source of protective factors that permit consumption of seemingly unsavory prey" [49] (see also [50]). As such, the risks and benefits of attacking different frog species may vary based on physiological responses both within predator and prey, which provides intriguing opportunities for future research.

Overall, the results of this study provide compelling evidence for ontogenetic changes to predatory responses in an eavesdropping predator. We propose that juvenile bats, through experience with calling prey, learn to identify the palatable species within their local anuran community, and based on prey profitability, adjust their responses to acoustic stimuli accordingly. While, to our knowledge, this is the first study to explicitly compare eavesdropping responses of juveniles and adult generalist predators, we expect similar processes to occur in other predators. Ultimately, our study highlights the critical role of experience and development in early life in shaping predatory and, more specifically, eavesdropping strategies in the wild.

Ethics. All procedures were approved by the Ministry of the Environment of Panamá (MiAmbiente permit numbers: SE/A-43-07, SE/A-91-09, SE/A-95-10, SE/A-6-11, SE/A-46-11, SE/A-94-11, SE/A-58-12) and the Smithsonian Tropical Research Institute (IACUC protocol numbers: 2007 14-06-15-07 and 20100816-1012-16).

Data accessibility. Data and code are provided as supplementary material [51].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

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Authors' contributions. L.S.J.: formal analysis, visualization, writing—original draft, writing—review and editing; M.T.O.: conceptualization, investigation, methodology, writing—review and editing; J.C.T.: conceptualization, investigation, methodology, writing—review and editing; M.J.R.: conceptualization, resources, writing—review and editing; X.E.B.: conceptualization, investigation, methodology, supervision, writing—original draft, writing—review and editing; R.A.P.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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References

1. Fay C, Young JK, Stankowich T. 2024 Aposematic learning in a mammalian predator–prey system. *Anim. Behav*. **212**, 39–48. (doi:10.1016/j.anbehav.2024.03.018)
2. Guilford T. 1988 The evolution of conspicuous coloration. *Am. Nat*. **131**, S7–S21. (doi:10.1086/284764)
3. McLellan CF, Scott-Samuel NE, Cuthill IC. 2021 Birds learn to avoid aposematic prey by using the appearance of host plants. *Curr. Biol*. **31**, 5364–5369.(doi:10.1016/j.cub.2021.09.048)
4. Schuler W, Roper TJ. 1992 Responses to warning coloration in avian predators. *Adv Stud Behav* **21**, 111–146.
5. White TE, Latty T, Umbers KDL. 2022 The exploitation of sexual signals by predators: a meta-analysis. *Proc. R. Soc. B* **289**, 20220444. (doi:10.1098/rspb.2022.0444)
6. Zuk M, Kolluru GR. 1998 Exploitation of sexual signals by predators and parasitoids. *Q. Rev. Biol*. **73**, 415–438. (doi:10.1086/420412)
7. Bernal XE, Page RA. 2023 Tactics of evasion: strategies used by signallers to deter eavesdropping enemies from exploiting communication systems. *Biol. Rev* **98**, 222–242. (doi:10.1111/brv.12904)
8. Smith SM. 1975 Innate recognition of coral snake pattern by a possible avian predator. *Science* **187**, 759–760. (doi:10.1126/science.187.4178.759)
9. Smith SM. 1977 Coral-snake pattern recognition and stimulus generalisation by naive great kiskadees (Aves: Tyrannidae). *Nature* **265**, 535–536. (doi:10.1038/265535a0)
10. Arnold SJ. 1977 Polymorphism and geographic variation in the feeding behavior of the garter snake *Thamnophis elegans*. *Science* **197**, 676–678. (doi:10.1126/science.197.4304.676)
11. Arnold SJ. 1992 Behavioural variation in natural populations. VI. Prey responses by two species of garter snakes in three regions of sympatry. *Anim. Behav*. **44**, 705–719. (doi:10.1016/s0003-3472(05)80297-0)
12. Galef BG, Laland KN. 2005 Social learning in animals: empirical studies and theoretical models. *BioScience* **55**, 489. (doi:10.1641/0006-3568(2005)055[0489:sliaes]2.0.co;2)
13. Kendal RL, Boogert NJ, Rendell L, Laland KN, Webster M, Jones PL. 2018 Social learning strategies: bridge-building between fields. *Trends Cogn. Sci*. **22**, 651–665. (doi:10.1016/j.tics.2018.04.003)
14. Brower LP, Cook LM, Croze HJ. 1967 Predator responses to artificial Batesian mimics released in a Neotropical environment. *Evolution* **21**, 11. (doi:10.2307/2406736)
15. Barber JR, Conner WE. 2007 Acoustic mimicry in a predator-prey interaction. *Proc. Natl Acad. Sci. USA* **104**, 9331–9334. (doi:10.1073/pnas.0703627104)
16. Hämäläinen L, Hoppitt W, Rowland HM, Mappes J, Fulford AJ, Sosa S, Thorogood R. 2021 Social transmission in the wild can reduce predation pressure on novel prey signals. *Nat. Commun*. **12**, 3978. (doi:10.1038/s41467-021-24154-0)
17. Hoppitt W, Brown G, Kendal R, Rendell L, Thornton A, Webster M, Laland K. 2008 Lessons from animal teaching. *Trends Ecol. Evol*. **23**, 486–493. (doi:10.1016/j.tree.2008.05.008)
18. Jones PL, Ryan MJ, Page RA. 2014 Population and seasonal variation in response to prey calls by an eavesdropping bat. *Behav. Ecol. Sociobiol*. **68**, 605–615. (doi:10.1007/s00265-013-1675-6)
19. Page RA, Ryan MJ. 2005 Flexibility in assessment of prey cues: frog-eating bats and frog calls. *Proc. R. Soc. B* **272**, 841–847. (doi:10.1098/rspb.2004.2998)
20. Page RA, Ryan MJ. 2006 Social transmission of novel foraging behavior in bats: frog calls and their referents. *Curr. Biol*. **16**, 1201–1205. (doi:10.1016/j.cub.2006.04.038)
21. Ryan MJ, Tuttle MD. 1983 The ability of the frog-eating bat to discriminate among novel and potentially poisonous frog species using acoustic cues. *Anim. Behav*. **31**, 827–833. (doi:10.1016/s0003-3472(83)80239-5)
22. Tuttle MD, Ryan MJ. 1981 Bat predation and the evolution of frog vocalizations in the Neotropics. *Science* **214**, 677–678. (doi:10.1126/science.214.4521.677)
23. Dixon MM, Jones PL, Ryan MJ, Carter GG, Page RA. 2022 Long-term memory in frog-eating bats. *Curr. Biol*. **32**, R557–R558. (doi:10.1016/j.cub.2022.05.031)
24. Hemingway CT, Ryan MJ, Page RA. 2020 State-dependent learning influences foraging behaviour in an acoustic predator. *Anim. Behav*. **163**, 33–38. (doi:10.1016/j.anbehav.2020.02.004)
25. Jones PL, Ryan MJ, Flores V, Page RA. 2013 When to approach novel prey cues? Social learning strategies in frog-eating bats. *Proc. R. Soc. B* **280**, 20132330. (doi:10.1098/rspb.2013.2330)
26. Brunet-Rossinni AK, Wilkinson GS. 2009 Methods for age estimation and the study of senescence in bats. In *Ecological and behavioral methods for the study of bats* (eds T Kunz, S Parsons), pp. 315–325. Baltimore, MD: Johns Hopkins University Press.
27. Flores V, Page RA. 2017 Novel odorous crust on the forearm of reproductive male fringe-lipped bats (*Trachops cirrhosus*). *J. Mammal*. **98**, 1568–1577. (doi:10.1093/jmammal/gyx137)
28. Toledo RC, Jared C. 1995 Cutaneous granular glands and amphibian venoms. *Comp. Biochem. Physiol. Part Physio.* **111**, 1–29. (doi:10.1016/0300-9629(95)98515-i)
29. Gómez-Feuillet L, O'Mara MT, Page RA. 2024 *Leptodactylus savagei*. *Herp Rev.* **55**, 73.
30. Limaverde PT, Nascimento NRF, Evangelista JSAM, Tomé AR, Fonteles MC, Santos CF, Cardi BA, Carvalho KM. 2009 Isolation and pharmacological effects of leptoxin, a novel proteic toxin from *Leptodactylus pentadactylus* skin secretion. *Toxicon* **54**, 531–538. (doi:10.1016/j.toxicon.2009.05.029)

31. Mikula P. 2015 Fish and amphibians as bat predators. *Eur. J. Ecol*. **1**, 71–80. (doi:10.1515/eje-2015-0010)
32. Legett HD, Page RA, Bernal XE. 2019 Synchronized mating signals in a communication network: the challenge of avoiding predators while attracting mates. *Proc. R. Soc. B* **286**, 20191067. (doi:10.1098/rspb.2019.1067)
33. Page RA, Schnelle T, Kalko EKV, Bunge T, Bernal XE. 2012 Sequential assessment of prey through the use of multiple sensory cues by an eavesdropping bat. *Naturwissenschaften* **99**, 505–509. (doi:10.1007/s00114-012-0920-6)
34. Trillo PA, Bernal XE, Caldwell MS, Halfwerk WH, Wessel MO, Page RA. 2016 Collateral damage or a shadow of safety? The effects of signalling heterospecific neighbours on the risks of parasitism and predation. *Proc. R. Soc. B* **283**, 20160343. (doi:10.1098/rspb.2016.0343)
35. Tuttle MD, Ryan MJ. 1982 The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. *Behav. Ecol. Sociobiol*. **11**, 125–131. (doi:10.1007/bf00300101)
36. Jones PL, Divoll TJ, Dixon MM, Aparicio D, Cohen G, Mueller UG, Ryan MJ, Page RA. 2020 Sensory ecology of the frog-eating bat, *Trachops cirrhosus*, from DNA metabarcoding and behavior. *Behav. Ecol*. **31**, 1420–1428. (doi:10.1093/beheco/araa100)
37. Ibañez RD, Rand AS, Jaramillo CA. 1999 *The amphibians of Barro Colorado Nature Monument, Soberanía National Park and adjacent areas*. Panamá, Republic of Panama: Smithsonian Tropical Research Institute.
38. Page RA, Ryan MJ. 2008 The effect of signal complexity on localization performance in bats that localize frog calls. *Anim. Behav*. **76**, 761–769. (doi:10.1016/j.anbehav.2008.05.006)
39. Jones PL, Hämsch F, Page RA, Kalko EKV, O'Mara MT. 2017 Foraging and roosting behaviour of the fringe-lipped bat, *Trachops cirrhosus*, on Barro Colorado Island, Panamá. *Acta Chiropterologica* **19**, 337–346. (doi:10.3161/15081109acc2017.19.2.010)
40. Kalko EKV, Friemel D, Handley CO, Schnitzler H. 1999 Roosting and foraging behavior of two neotropical gleaning bats, *Tonatia silvicola* and *Trachops cirrhosus* (Phyllostomidae). *Biotropica* **31**, 344–353. (doi:10.1111/j.1744-7429.1999.tb00146.x)
41. Falk JJ, ter Hofstede HM, Jones PL, Dixon MM, Faure PA, Kalko EKV, Page RA. 2015 Sensory-based niche partitioning in a multiple predator–multiple prey community. *Proc. R. Soc. B* **282**, 20150520. (doi:10.1098/rspb.2015.0520)
42. Jones PL, Page RA, Hartbauer M, Siemers BM. 2011 Behavioral evidence for eavesdropping on prey song in two Palearctic sibling bat species. *Behav. Ecol. Sociobiol*. **65**, 333–340. (doi:10.1007/s00265-010-1050-9)
43. Fonseca BDS, Soto-Centeno JA, Simmons NB, Ditchfield AD, Leite YLR. 2024 A species complex in the iconic frog-eating bat *Trachops cirrhosus* (Chiroptera, Phyllostomidae) with high variation in the heart of the Neotropics. *Am. Mus. Novit*. **2024**. (doi:10.1206/4021.1)
44. Trillo PA, Athanas KA, Goldhill DH, Hoke KL, Funk WC. 2013 The influence of geographic heterogeneity in predation pressure on sexual signal divergence in an Amazonian frog species complex. *J. Evol. Biol*. **26**, 216–222. (doi:10.1111/jeb.12041)
45. Fugère V, Teague O'Mara M, Page RA. 2015 Perceptual bias does not explain preference for prey call adornment in the frog-eating bat. *Behav. Ecol. Sociobiol*. **69**, 1353–1364. (doi:10.1007/s00265-015-1949-2)
46. Bernal XE, Page RA, Rand AS, Ryan MJ. 2007 Cues for eavesdroppers: do frog calls indicate prey density and quality? *Am. Nat*. **169**, 409–415. (doi:10.1086/510729)
47. Jones PL, Farris HE, Ryan MJ, Page RA. 2013 Do frog-eating bats perceptually bind the complex components of frog calls? *J. Comp. Physiol*. **199**, 279–283. (doi:10.1007/s00359-012-0791-5)
48. Davis LR *et al*. 2016 Host defense skin peptides vary with color pattern in the highly polymorphic red-eyed treefrog. *Front. Ecol. Evol*. **4**. (doi:10.3389/fevo.2016.00097)
49. Tandler B, Nagato T, Phillips CJ. 1997 Ultrastructure of the unusual accessory submandibular gland in the fringe-lipped bat, *Trachops cirrhosus*. *Anat. Rec.* **248**, 164–175. (doi:10.1002/(sici)1097-0185(199706)248:23.0.co;2-t)
50. Phillips CJ, Tandler B, Pinkstaff CA. 1987 Unique salivary glands in two genera of tropical microchiropteran bats: an example of evolutionary convergence in histology and histochemistry. *J. Mammal*. **68**, 235–242. (doi:10.2307/1381462)
51. James LS, O'Mara MT, Touchon JC, Ryan M, Bernal X, Page RA. 2025 Supplementary material from: The ontogeny of decision-making in an eavesdropping predator. Figshare. (doi:10.6084/m9.figshare.c.7750321)

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