

## NOTE

# Prey Exploits the Auditory Illusions of Eavesdropping Predators

Henry D. Legett,<sup>1,\*</sup> Claire T. Hemingway,<sup>2</sup> and Ximena E. Bernal<sup>1,3</sup>

1. Department of Biological Sciences, Purdue University, West Lafayette, Indiana 47907; 2. Department of Integrative Biology, University of Texas, Austin, Texas 78712; 3. Smithsonian Tropical Research Institute, Balboa, Ancón, Panama

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**ABSTRACT:** Mating signals have evolved to attract target receivers, even to the point of exploiting receivers through perceptual manipulation. Signals, however, can also expose signalers to nontarget receivers, including predators and parasites, and thus have also evolved to decrease enemy attraction. Here we show that male tree frogs (*Smilisca sila*) reduce their attractiveness to eavesdropping enemies (bats and midges) by overlapping their calls at near-perfect synchrony with the calls of neighboring conspecifics. By producing calls that closely follow those of other males, synchronizing *S. sila* take advantage of an auditory illusion where enemies are more attracted to the leading call. Female *S. sila*, however, are less susceptible to this illusion. Thus, synchronization among signaling males can result in acoustic crypsis from predators without affecting female attraction. Given the widespread use of conspicuous mating signals and eavesdropping enemies, perceptual exploitation of eavesdroppers is likely a common driver of signal evolution.

**Keywords:** animal communication, communication network, eavesdroppers, sensory exploitation, synchrony, illusion.

## Introduction

Mating signals can both evolve to advertise traits that benefit female reproductive success and to exploit preexisting perceptual inaccuracies without necessarily providing a direct benefit to the female (Ryan 1990; Christy 1995; Endler and Basolo 1998; Ryan and Cummings 2013). Females, however, are not the only receivers driving signal evolution. Mating signals also expose signalers to natural enemies, such as eavesdropping predators and parasites (Zuk and Kolluru 1998). While selective pressures imposed by female perceptual systems have received considerable attention (reviewed in Ryan and Cummings 2013), there has been little consideration of how exploiting perceptual misjudgments of eavesdroppers can also influence signal evolution.

\* Corresponding author; email: [hlegett@purdue.edu](mailto:hlegett@purdue.edu).

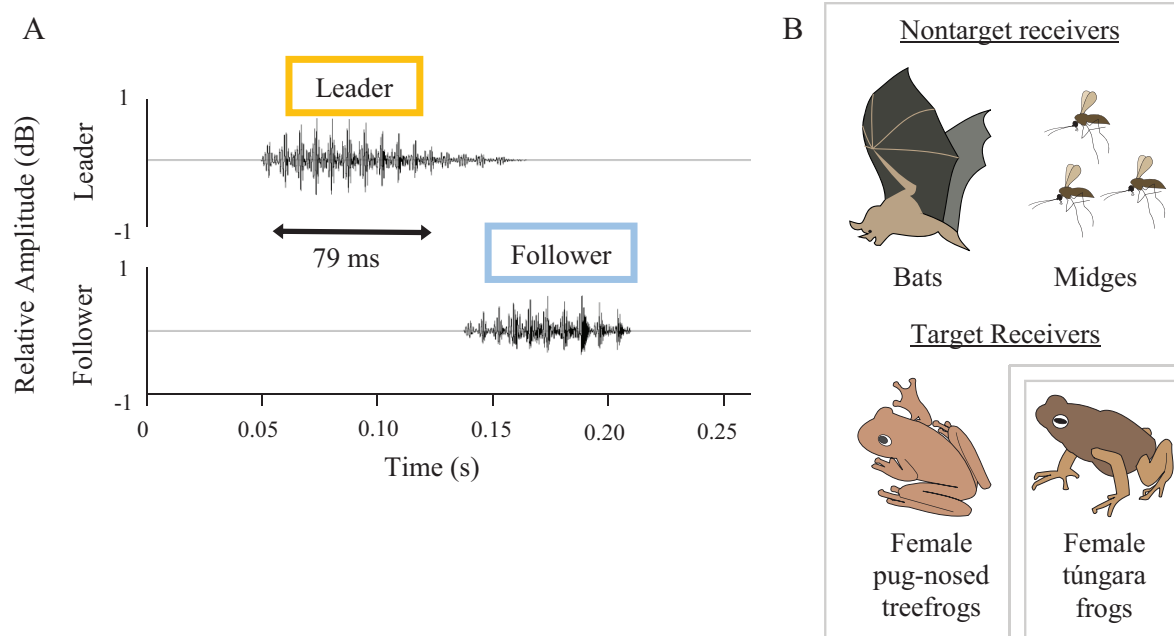
**ORCID:** Legett, <https://orcid.org/0000-0001-9005-8641>; Hemingway, <https://orcid.org/0000-0002-0901-1553>; Bernal, <https://orcid.org/0000-0001-6155-5980>.

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Antagonistic selection from eavesdroppers can result in unexpected signal characteristics, such as reduced signal conspicuousness. A common example of this adaptation is the use of private communication channels between conspecifics in which the signal escapes the range of sensitivity of their predator, such as visual signaling in the ultraviolet range (Cummings et al. 2003). In extreme cases, complete loss of the signal can occur, as in Hawaiian field crickets (*Teleogryllus oceanicus*) that are parasitized by eavesdropping flies (*Ormia ochracea*; Zuk et al. 2006). Avoiding the sensory range of natural enemies is not the only way to reduce detection, as signals could instead evolve to exploit perceptual errors of eavesdropping enemies. Here, we investigate this hypothesis and provide evidence of signalers exploiting the sensory systems of eavesdropping predators and parasites through an auditory illusion. Specifically, we examine how signal synchronization in pug-nosed tree frogs (*Smilisca sila*) can result in acoustic crypsis from such natural enemies.

When two sounds are closely synchronized, humans and other acoustically sensitive animals exhibit a perceptual localization bias toward the first leading sound over the following sound (Wallach et al. 1949). Through this precedence effect, even when the sources are separated in space, the receiver perceives both sounds as having originated from the source of the leading sound. By producing signals closely synchronized with those of neighboring conspecifics, signaling males could create an illusion that obscures the locational information of their signals from receivers. Because of the precedence effect, females typically favor leading signals over signals produced by following males, and as a result, males producing auditory displays typically avoid overlapping their mating signals (Greenfield et al. 1997; Gerhardt and Huber 2002, pp. 263–277). Synchronized signals, however, could also obscure the location of the following male from nontarget receivers. Despite the potential cost to females, male pug-nosed tree frogs produce calls in near-perfect synchrony with neighboring conspecifics (fig. 1A), overlapping call production at extremely short latencies (Ryan 1986). Males of this species, however, are also preyed upon by frog-eating bats (*Trachops cirrhosus*) and frog-biting



**Figure 1:** A, Oscillograms of leading and following calls of two male pug-nosed tree frogs. B, Target and nontarget call receivers included in this study. Calls are synchronized with 79 ms of latency, the observed natural average in this species (Ryan 1986).

midges (*Corethrella* spp.), both of which use calls to localize the frogs. Earlier work (Tuttle and Ryan 1982) revealed that eavesdropping bats and midges preferentially attack choruses of pug-nosed tree frogs calling artificially out-of-synchrony over synchronized choruses, as males naturally call in this species. It is unclear, however, how call order between individual males synchronizing their calls within the chorus affects receiver attraction. To examine this case of potential acoustic crypsis, we investigate how these bats and midges respond to the illusion generated by overlapping leading and following signals. Ultimately, we seek to determine whether these predators experience a precedence effect with synchronized calls. We predict that males producing following calls exploit the precedence effect in their eavesdropping enemies, reducing their attraction of both nontarget receivers compared with the calls of leading males. It is puzzling, however, how such signal crypsis could evolve if it also comes at a cost to mate attraction. We therefore also investigate how target receivers, conspecific females, respond to synchronization.

### Methods

Following previously established methods (frogs: Dyson and Passmore 1988; midges: Bernal et al. 2006; bats: Page and Ryan 2008), we conducted a series of both laboratory and field acoustic playback experiments to assess the leader-follower call preferences in the target receiver (female frogs) and

nontarget eavesdroppers (bats and midges). In addition, we established a reference for the strength or weakness of the precedence effect in female pug-nosed tree frogs by also assessing leader-follower preferences of female frogs from a sympatric anuran species in which males do not synchronize their calls, the túngara frog (*Engystomops pustulosus*). In total, we performed four independent phonotaxis experiments: three testing bat, midge, and female pug-nosed tree frog preferences broadcasting male pug-nosed tree frog calls and one testing female túngara frog preferences using male túngara frog calls (fig. 1B). All experiments were conducted in and around Gamboa, Republic of Panama (9°07.0'N, 79°41.9'W). For each experiment, a pair of speakers broadcast synchronized recordings of male frog calls with 79 ms of latency (average for pug-nosed tree frogs; Ryan 1986). Within a trial, one speaker out of the set always broadcast leading calls and the other speaker always broadcast following calls. Which of the two speakers broadcast which treatment, leading or following, was randomized for each trial to account for any side biases in receiver attraction. The speakers were placed at a distance that roughly matched the spacing between neighboring males in a chorus of either species (for examples of receiver phonotaxis recorded during the experiments, see video 1, available online).

A sample of 10 recorded calls, each one from different males, were used to build a stimulus library of 90 different leader-follower combinations. In this way, two libraries were built—one for synchronized pug-nosed tree frog calls and



**Video 1:** Still photograph from a video (available online) showing examples of receiver phonotaxis recorded during the experiments. The video contains the following clips: (1) frog-eating bat example no. 1, (2) frog-eating bat example no. 2, (3) female pug-nosed tree frog, and (4) female túngara frog.

one for synchronized túngara frog calls. For each trial, stimuli were randomly drawn from the respective library. Only one stimuli, one set of synchronized calls, was used per trial. For the pug-nosed tree frog stimuli, only recordings of non-overlapped calls were used to avoid any prior artifacts from acoustic interference. Recordings were edited using Cool-Edit2000 (Syntrillium Software), and stimuli were broadcast at a rate of one call every 2 s, at an amplitude of 75 dB SPL re. 20  $\mu$ P at 1 m from the speakers measured at ground level.

#### *Frog-Eating Bat Preference*

Ten wild-caught bats were captured from June 1 to August 16, 2017, using mist nets set along streams and small ponds. Each bat was marked with a passive transponder (PIT tags, Trovan), and tested individually in a 5  $\times$  5  $\times$  2.5-m outdoor flight cage between 1900 and 0200 h. During the experiments, the bats were presented with two Fostex speakers (model FE103En; Foster Electric, Tokyo) baited with fish (following Page and Ryan 2006; Hemingway et al. 2018) and spaced 1.5 m apart, broadcasting leading and following pug-nosed tree frog calls. Each bat was repeatedly tested using a new set of two recordings for a total of 10 consecutive choices ( $N = 100$  choices). A choice was defined by flight within 50 cm of a speaker (Hemingway et al. 2018). The number of times out of the 10 trials that a bat chose either leading or following calls was recorded. The bats were returned to their initial capture location following experiments.

#### *Frog-Biting Midge Preference*

Frog-biting midges were collected from January 11 to March 5, 2017, using acoustic insect traps (McKeever and Hartberg 1980) placed over two Pignose portable amplifier speakers (model 7-100; Pignose-Gorilla, North Las Vegas,

Nevada) spaced 1 m apart. Collection sites were chosen randomly in the forest within 100 m of a water source with breeding pug-nosed tree frogs. The set of speakers broadcast leading and following pug-nosed tree frog calls, randomly drawn from the stimulus library. The two speakers with their corresponding traps were run once per night for 45 min following sunset. A total of 1,095 frog-biting midges were collected over a sampling period of 21 nights. The number of midges attracted each night to either the leading or following calls was used as an indicator of preference. Following their collection, frog-biting midges were counted and preserved in 75% ethanol for identification to species. A representative sample of the specimens was mounted and deposited in the collections at Purdue University.

#### *Female Frog Preference*

Phonotaxis experiments using female pug-nosed tree frogs ( $n = 23$ ) were conducted from February 2 to March 4, 2017. Pairs of frogs were collected in amplexus from natural occurring choruses and transported to a 2  $\times$  3-m semianechoic chamber (ETS-Lindgren, Cedar Park, Texas). Females found in amplexus were used because they are highly receptive to male calls (Lynch et al. 2005). Immediately before testing, females were separated from the males and placed in the chamber under an acoustically transparent cup 1.5 m from a set Pignose speakers spaced 1 m apart and broadcasting leading and following pug-nosed tree frog calls. Females were kept under the cup for 1 min to adjust to the chamber before being released. Following standard rules used in phonotaxis experiments with anurans (Ryan and Rand 1990), a choice for either the leading or following call was scored after the female approached within 10 cm of a speaker. Females were tested once and released with their males at the end of the night. This experiment was repeated from October 17 to October 25, 2017, using female túngara frogs ( $n = 40$ ) and broadcasts of synchronized túngara frog calls. Although leader-follower preferences have previously been assessed in túngara frogs (Schwartz and Rand 1991; unpublished data discussed in Greenfield and Rand 2000), we aimed to test túngara frogs using an experimental design that mirrored the methods used here for pug-nosed tree frogs.

#### *Statistical Analyses*

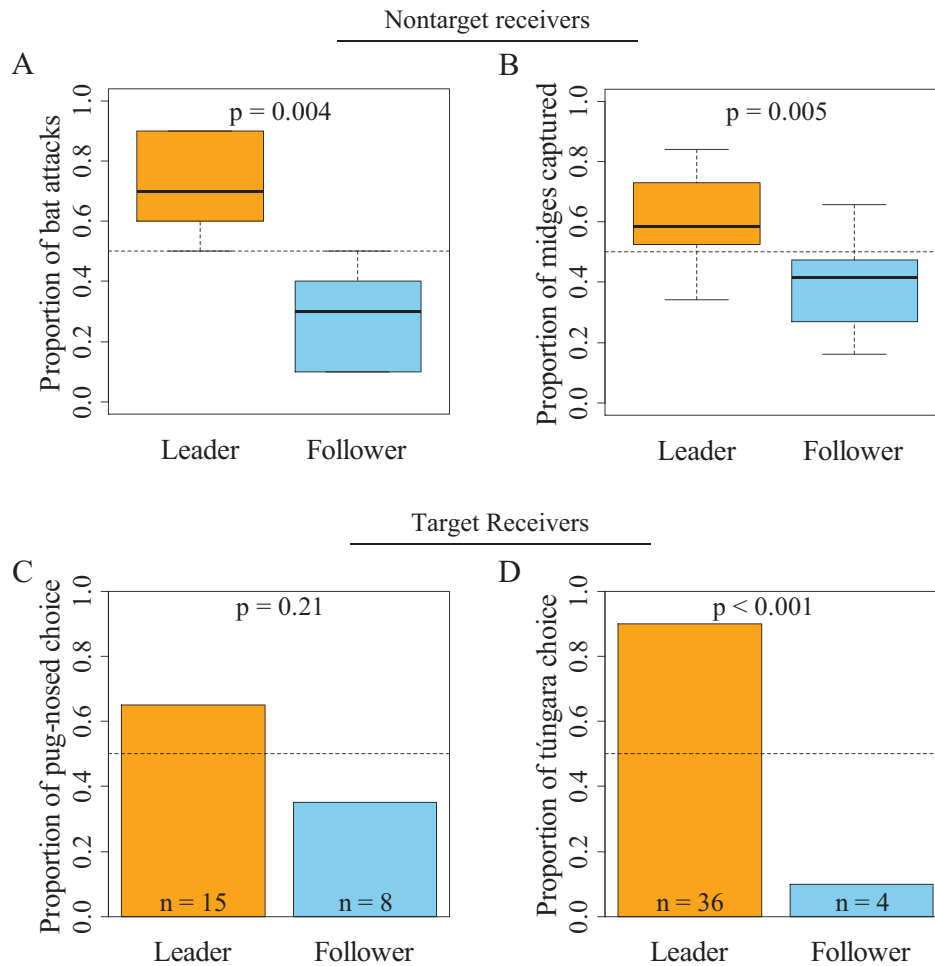
All analyses were conducted in R version 3.5.2 (R Development Core Team 2015). Bat and midge preferences were independently analyzed using a two-tailed exact symmetry tests in the R package coin (Hothorn et al. 2008), testing the null hypothesis that preference was even between the leading and following calls. For the bat experiment, the number of choices for leading and following calls were compared, with the repeated measurements blocked within

each individual bat ( $N = 100$  choices,  $n = 10$  choices/individual). For the midge preference experiment, the number of midges attracted to the leading and following calls was compared, blocked within each night ( $n = 21$  nights). For both female preference experiments, pug-nosed tree frog ( $n = 23$  frogs) and túngara frog ( $n = 40$  frogs), choice for either leading or following calls was analyzed using a two-tailed exact binomial choice test, again testing the null hypothesis that preference was even between the leading and following calls. Additionally, given the smaller sample size for the female pug-nosed tree frog experiment, concerns about a potential type II error were excluded using a statistical power analysis using G\*Power 3.1 (Faul et al. 2009). Data underlying these statistical analyses have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.8w9ghx3gs>; Legett et al. 2019).

**Results**

Both bats and midges, the nontarget eavesdropping receivers, had a significant preference for leading pug-nosed tree frog calls over following calls. Frog-eating bats chose the speaker broadcasting leading calls on average 70% of the time ( $Z = 2.65, P = .004$ ; fig. 2A). Leading speakers also attracted an average of 55% more midges per night than speakers broadcasting following calls ( $31.67 \pm 11.60$  midges for leading calls vs.  $20.48 \pm 5.05$  midges for following calls;  $Z = 2.66, P = .005$ ; fig. 2B).

Female pug-nosed tree frogs, the target receivers, displayed no significant preference for leading or following calls, with only 15 of the 23 females tested choosing the leading call ( $P = .21$ ; fig. 2C). In contrast, female túngara frogs, a nonsynchronous species, displayed a strong preference



**Figure 2:** Proportion of nontarget (A, bats; B, midges) and target (C, female pug-nosed frogs) receivers that selected for leading or following recorded calls of male pug-nosed tree frogs. The preferences of another target receiver, female túngara frogs (D), were assessed using male túngara frog calls.

with 36 of the 40 females choosing leading conspecific calls ( $P < .001$ ; fig. 2D).

Using the effect size of the female túngara frog choice experiment for comparison, the female pug-nosed tree frog preference experiment had adequate statistical power ( $1 - \beta = 0.99$ ,  $\alpha = 0.05$ , effect size = 0.40). In addition to female túngara frogs, a similar level of leading call preference has been found in other anuran species (effect size =  $0.35 \pm 0.06$  calculated from Schwartz 1986; Dyson and Passmore 1988; Grafe 1996; Bosch and Márquez 2002; Marshall and Gerhardt 2010; Reichert et al. 2016). If female pug-nosed tree frogs had leader-follower preferences comparable to female túngara frogs and other anuran species tested to date, we would expect 20 or 21 of the 23 tested female pug-nosed tree frog to prefer leading calls.

### Discussion

Our results from the bat and midge preference experiments suggest that both predatory eavesdroppers are vulnerable to the precedence effect illusion and thus susceptible to exploitation. For acoustic receivers in general, the precedence effect is thought to be an adaptation for successfully localizing sounds in structurally complex environments, where reflections and reverberations carry spatial cues unrelated to the source of the signal (Litovsky et al. 1999). In these acoustic situations, the auditory system gives perceptual dominance of spatial information to the first arriving signal. Both the eavesdropping bats and midges forage in dense forest habitats, relying on their ability to detect and localize frog calls to find their prey. Therefore, despite drastic differences between perceptual systems, it is not unexpected that these two receivers experience this auditory effect.

Similar to the acoustic challenges facing the predators, female frogs must also localize calls in structurally complex environments to find mates and are therefore also expected to experience a precedence effect. This prediction is confirmed here in the strong leading call preference displayed by female túngara frogs and is characteristic of the response of females from most anuran species examined to date (e.g., Schwartz 1986; Dyson and Passmore 1988; Grafe 1996; Bosch and Márquez 2002; Marshall and Gerhardt 2010; Reichert et al. 2016). For male frogs of these species, benefits from exploiting the precedence effect in eavesdroppers by synchronizing are not balanced out by the substantial cost imposed on the male producing the less attractive following calls. Female pug-nosed tree frogs, in contrast, break from this expected bias for leading signals, suggesting that they do not experience a precedence effect or that the strength of this effect is perceptually reduced. Thus, unlike túngara frogs, male pug-nosed tree frogs producing following calls benefit from reduced eavesdropper

attraction without suffering the cost of reduced female attraction. Why then, would a male pug-nosed tree frog produce leading calls? With the reduced cost to producing following calls but higher cost of producing leading calls, males compete in a “war of attrition” game (Grafe 2003) in which they try to avoid being the first to call. Eventually, however, males must produce calls to attract mates. Thus, males that produce the first leading calls lose this intra-sexual competition. As a result, pug-nosed tree frog choruses are characterized by long periods of silence punctuated by short, sporadic bouts of synchronized calls (Tuttle and Ryan 1982). Whether certain males within the chorus always end up leading in this game is currently unknown. Recent advances in sound-visualization techniques (Mizumoto et al. 2011) may help investigate the signaling interactions between multiple synchronizing males.

In addition to female pug-nosed tree frogs, atypical or reversed leader-follower preferences have been observed in other synchronizing anuran species (*Dendropsophus ebraccatus*: Wells and Schwartz 1984; *Kassina fusca*: Grafe 1999). Therefore, a loss of this preference, overcoming the precedence effect illusion, may be key to the evolution and maintenance of this signaling strategy. How females of synchronizing species are able to overcome the precedence effect is still a mystery. Studies that examine the auditory physiology, specifically temporal processing, of such species and their nonsynchronous congeners would provide insight into the mechanisms underlying the use of synchronized mating signals. Overall, obtaining a thorough understanding of the evolutionary drivers that shape signals and signaling strategies requires an understanding of the individual and combined selective pressures imposed by target and nontarget receivers. A communication network approach (McGregor and Peake 2000) examining selective pressure from multiple receivers, as the one used here, provides important insights into understanding these processes that shape signal evolution. Further studies that provide a phylogenetic framework to understand the sequence in which costs and benefits from multiple receivers unfolded is also necessary to better understand the evolution of signals.

Finally, while this study focuses on the male vocal behavior of synchronization, the costs and benefits to overcoming the precedence effect for the female receiver warrants corresponding consideration. By not experiencing a precedence effect, females may be able to discriminate between preferred and nonpreferred males independent of call timing (Táranó 2015; Schwartz and Serratto Del Monte 2018). In addition, since female frogs can avoid approaching males associated with higher perceived predation risk (Bonachea and Ryan 2011), and males with leading calls are more attractive to predators, overcoming the precedence effect may allow females to reduce their risk of predation. Further studies from the female’s perspective,



in particular examining the predation rates associated with different mate choices, are needed to better understand the trade-offs of signal synchronization and other signaling strategies.

We show that by synchronizing their calls with those of neighbor males, pug-nosed tree frogs exploit the sensory perspective of eavesdropping enemies, yielding fewer attacks. Thus, our results suggest that misjudgments in sensory systems of predators can play a direct role in shaping mate-signaling strategies. While prey manipulation of predators' sensory systems to misdirect or reduce detection has long been acknowledged (Kelley and Kelley 2013; Rubin et al. 2018), this study provides the first case of perceptual manipulation of eavesdroppers through illusions of mating signals. Mating signals are at the intersection of natural and sexual selection, driven to increase attraction of target receivers but simultaneously avoid the attraction of nontargets. Therefore, as perceptual exploitation of mates by signaling males has proved valuable to understanding signal evolution (Endler and Basolo 1998; Ryan and Cummings 2013), exploitations of eavesdropping predators are also likely to provide valuable insights. Ultimately, we show that auditory illusions can be exploited to decrease predation without decreasing mate attraction. Similar sensory manipulations of predatory eavesdroppers are expected in other organisms and across sensory modalities beyond the acoustic realm.

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#### Literature Cited

- Bernal, X. E., A. S. Rand, and M. J. Ryan. 2006. Acoustic preferences and localization performance of blood-sucking flies (*Cordylobes* Coquillett) to túngara frog calls. *Behavioral Ecology* 17:709–715.
- Bonachea, L. A., and M. J. Ryan. 2011. Simulated predation risk influences female choice in túngara frogs, *Physalaemus pustulosus*. *Ethology*, 117:400–407.
- Bosch, J., and R. Márquez. 2002. Female preference function related to precedence effect in an amphibian anuran (*Alytes cisternasii*): tests with non-overlapping calls. *Behavioral Ecology* 13:149–153.
- Christy, J. H. 1995. Mimicry, mate choice, and the sensory trap hypothesis. *American Naturalist* 146:171–181.
- Cummings, M. E., G. G. Rosenthal, and M. J. Ryan. 2003. A private ultraviolet channel in visual communication. *Proceedings of the Royal Society B* 270:897–904.
- Dyson, M. L., and N. I. Passmore. 1988. Two-choice phonotaxis in *Hyperolius marmoratus* (Anura: Hyperoliidae): the effect of temporal variation in presented stimuli. *Animal Behaviour* 36:648–652.
- Endler, J. A., and A. L. Basolo. 1998. Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution*, 13:415–420.
- Faul, F., E. Erdfelder, A. Buchner, and A. G. Lang. 2009. Statistical power analyses using G\*Power 3.1: tests for correlation and regression analyses. *Behavior Research Methods* 41:1149–1160.
- Gerhardt, H. C., and F. Huber. 2002. *Acoustic communication in insects and anurans: common problems and diverse solutions*. University of Chicago Press, Chicago.
- Grafe, T. U. 1996. The function of call alternation in the African reed frog (*Hyperolius marmoratus*): precise call timing prevents auditory masking. *Behavioral Ecology and Sociobiology* 38:149–158.
- . 1999. A function of synchronous chorusing and a novel female preference shift in an anuran. *Proceedings of the Royal Society B* 266:2331–2336.
- . 2003. Synchronized interdigitated calling in the Kuvangu running frog, *Kassina kuvangensis*. *Animal Behaviour* 66:127–136.
- Greenfield, M. D., and A. S. Rand. 2000. Frogs have rules: selective attention algorithms regulate chorusing in *Physalaemus pustulosus* (Leptodactylidae). *Ethology* 106:331–347.
- Greenfield, M. D., M. K. Tourtellot, and W. A. Snedden. 1997. Precedence effects and the evolution of chorusing. *Proceedings of the Royal Society B* 264:1355–1361.
- Hemingway, C. T., M. J. Ryan, and R. A. Page. 2018. Cognitive constraints on optimal foraging in frog-eating bats. *Animal Behaviour* 143:43–50.
- Hothorn, T., K. Hornik, M. A. van de Wiel, and A. Zeileis. 2008. Implementing a class of permutation tests: the coin package. *Journal of Statistical Software* 28:1–23.
- Kelley, L. A., and J. L. Kelley. 2013. Animal visual illusion and confusion: the importance of a perceptual perspective. *Behavioral Ecology* 25:450–463.
- Legett, H. D., C. T. Hemingway, and X. E. Bernal. 2019. Data from: Prey exploits the auditory illusions of eavesdropping predators. *American Naturalist*, Dryad Digital Repository, <https://doi.org/10.5061/dryad.8w9ghx3gs>.
- Litovsky, R. Y., H. S. Colburn, W. A. Yost, and S. J. Guzman. 1999. The precedence effect. *Journal of the Acoustical Society of America* 106:1633–1654.
- Lynch, K. S., A. S. Rand, M. J. Ryan, and W. Wilczynski. 2005. Plasticity in female mate choice associated with changing reproductive states. *Animal Behaviour* 69:689–699.

- Marshall, V. T., and H. C. Gerhardt. 2010. A precedence effect underlies preferences for calls with leading pulses in the grey treefrog, *Hyla versicolor*. *Animal Behaviour* 80:139–145.
- McGregor, P. K., and T. M. Peake. 2000. Communication networks: social environments for receiving and signalling behaviour. *Acta Ethologica* 2:71–81.
- McKeever, S., and W. K. Hartberg. 1980. An effective method for trapping adult female *Corethrella* (Diptera: Chaoboridae). *Mosquito News* 20:111–112.
- Mizumoto, T., I. Aihara, T. Otsuka, R. Takeda, K. Aihara, and H. G. Okuno. 2011. Sound imaging of nocturnal animal calls in their natural habitat. *Journal of Comparative Physiology A*, 197:915–921.
- Page, R. A., and M. J. Ryan. 2006. Social transmission of novel foraging behavior in bats: frog calls and their referents. *Current Biology* 16:1201–1205.
- . 2008. The effect of signal complexity on localization performance in bats that localize frog calls. *Animal Behaviour* 76:761–769.
- R Development Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Reichert, M. S., L. B. Symes, and G. Höbel. 2016. Lighting up sound preferences: cross-modal influences on the precedence effect in treefrogs. *Animal Behaviour* 119:151–159.
- Rubin, J. J., C. A. Hamilton, C. J. McClure, B. A. Chadwell, A. Y. Kawahara, and J. R. Barber. 2018. The evolution of anti-bat sensory illusions in moths. *Science Advances* 4:eaar7428.
- Ryan, M. J. 1986. Synchronized calling in a treefrog (*Smilisca sila*). *Brain, Behavior and Evolution* 29:196–206.
- . 1990. Sexual selection, sensory systems and sensory exploitation. Pages 157–195 in D. Futuyma and J. Antonovic, eds. *Oxford Surveys in Evolutionary Biology*. Vol. 7. Oxford, Oxford University Press.
- Ryan, M. J., and A. S. Rand. 1990. The sensory basis of sexual selection for complex calls in the túngara frog, *Physalaemus pustulosus* (sexual selection for sensory exploitation). *Evolution* 44:305–314.
- Ryan, M. J., and M. E. Cummings. 2013. Perceptual biases and mate choice. *Annual Review of Ecology, Evolution, and Systematics* 44:437–459.
- Schwartz, J. J. 1986. Male calling behavior and female choice in the Neotropical treefrog *Hyla microcephala*. *Ethology*, 73:116–127.
- Schwartz, J. J., and A. S. Rand. 1991. The consequences for communication of call overlap in the Túngara frog, a Neotropical anuran with a frequency-modulated call. *Ethology* 89:73–83.
- Schwartz, J. J., and M. E. Serratto Del Monte. 2018. Spatially-mediated call pattern recognition and the cocktail party problem in treefrog choruses: can call frequency differences help during signal overlap? *Bioacoustics*, 28:312–328.
- Tárano, Z. 2015. Choosing a mate in a cocktail party-like situation: the effect of call complexity and call timing between two rival males on female mating preferences in the túngara frog *Physalaemus pustulosus*. *Ethology*, 121:749–759.
- Tuttle, M. D., and M. J. Ryan. 1982. The role of synchronized calling, ambient light, and ambient noise, in anti-bat-predator behavior of a treefrog. *Behavioral Ecology and Sociobiology* 11:125–131.
- Wallach, H., E. B. Newman, and M. R. Rosenzweig. 1949. A precedence effect in sound localization. *Journal of the Acoustical Society of America* 21:468–468.
- Wells, K. D., and J. J. Schwartz. 1984. Vocal communication in a Neotropical treefrog, *Hyla ebraccata*: aggressive calls. *Behaviour* 91:128–145.
- Zuk, M., and G. R. Kolluru. 1998. Exploitation of sexual signals by predators and parasitoids. *Quarterly Review of Biology* 73:415–438.
- Zuk, M., J. T. Rotenberry, and R. M. Tinghitella. 2006. Silent night: adaptive disappearance of a sexual signal in a parasitized population of field crickets. *Biology Letters* 2:521–524.

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Male pug-nosed treefrog (*Smilisca sila*) being bitten by eavesdropping frog-biting midges (*Corethrella* spp.). Photo credit: Henry D. Legett.