

Social Transmission of Novel Foraging Behavior in Bats: Frog Calls and Their Referents

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Summary

The fringe-lipped bat, *Trachops cirrhosus*, uses prey-emitted acoustic cues (frog calls) to assess prey palatability [1]. Previous experiments show that wild *T. cirrhosus* brought into the laboratory are flexible in their ability to reverse the associations they form between prey cues and prey quality [2]. Here we asked how this flexibility can be achieved in nature. We quantified the rate at which bats learned to associate the calls of a poisonous toad species with palatable prey by placing bats in three groups: (a) social learning, in which a bat inexperienced with the novel association was allowed to observe an experienced bat; (b) social facilitation, in which two inexperienced bats were presented with the experimental task together; and (c) trial-and-error, in which a single inexperienced bat was presented with the experimental task alone. In the social-learning group, bats rapidly acquired the novel association in an average of 5.3 trials. In the social-facilitation and trial-and-error groups, most bats did not approach the call of the poisonous species after 100 trials. Thus, once acquired, novel associations between prey cue and prey quality could spread rapidly through the bat population by cultural transmission. This is the first case to document predator social learning of an acoustic prey cue.

Results and Discussion

Social learning can expand the foraging repertoire of a given individual and enhance predator foraging success [3–5]. Numerous studies have demonstrated the ability of predators to learn socially about prey cues in the olfactory and visual modalities (see [5] for review). Predator social learning of acoustic prey cues, however, has not been documented. Here we test the ability of the predatory bat, *T. cirrhosus*, to acquire a novel acoustic association for prey via social learning.

T. cirrhosus has a unique ability among bats to prey on frogs by listening to the advertisement calls male frogs produce to attract their mates [1]. In a previous study, we investigated the associations *T. cirrhosus* forms between prey cues (species-specific prey mating call) and

prey palatability [2]. Using a fading-conditioning paradigm [6], we were able to rapidly reverse the bats' assessment of palatable and poisonous prey.

Here we ask whether this flexibility is part of the bats' natural foraging repertoire and to what degree novel associations between prey cue and prey quality can be culturally transmitted. To address these questions, we quantified the rate of acquisition of a novel foraging behavior in three learning groups: (a) a social-learning group, (b) a social-facilitation group, and (c) a trial-and-error group. The target foraging behavior was the bats' ability to learn to associate the calls of the sympatric cane toad, *Bufo marinus*, with a palatable food reward. *B. marinus* is both highly poisonous and far too large for a *T. cirrhosus* to eat, so on two accounts it should be an unsuitable prey item. The criterion for task acquisition was flying to and landing on a speaker broadcasting toad calls in three consecutive trials.

We first conducted baseline tests with all bats to determine initial responses to *B. marinus* calls. None of the bats showed any initial response to *B. marinus* calls. We then tested for social learning by allowing an inexperienced bat to observe the foraging behavior of an experienced bat (tutor) that had already acquired the novel association. The first tutor learned to associate toad calls with a palatable food reward via a fading-conditioning technique (for methods, see [2]). Subsequent tutors acquired the association via social learning, such that the test bat in one experiment became the tutor in the next experiment.

The novel foraging association was transmitted successfully among all bats in the social-learning group ($n = 10$). There were two series of sequential interactions, or "chains" (Figure 1). The first chain consisted of two social-learning transmissions among three bats. The third bat died in captivity, and so the fourth bat was conditioned via fading, initiating a second chain of eight social-transmission events among nine bats, at which point we halted the experiment. Bats in the social-learning group acquired the novel foraging task in 5.3 ± 1.7 trials (mean \pm SEM, range = 1–11 trials, Figure 2). There was no degradation in the rate of acquisition from bat to bat (Pearson product-moment correlation: $r = 0.314$, $p = 0.377$; Figure 1).

To control for possible motivational effects associated with the mere presence of a second bat [7] in the social-facilitation group, we quantified the rate of acquisition of a test bat housed with an inexperienced conspecific ($n = 5$). In addition, in the trial-and-error group we quantified the rate of acquisition of bats housed alone, when the only possibility for task acquisition was individual learning ($n = 5$). Rates of task acquisition were significantly slower for these two groups in comparison with the social-learning group (Kruskal Wallis test: $H = 15.28$, $p < 0.001$, Figure 2). There was no significant difference in the rate of acquisition between the social-facilitation group and the trial-and-error group (mean trials to acquisition \pm SEM: 96.8 ± 3.2 and

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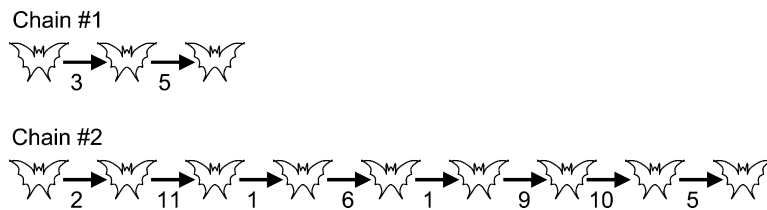


Figure 1. Chains of Transfer in the Social Learning Group

Arrows indicate the transmission of the novel foraging behavior; the numbers underneath the arrows indicate the number of trials required to reach acquisition criterion for each bat. After testing, the current test bat became the tutor for the next test bat.

96.2 ± 3.8, respectively. Mann-Whitney U test: U = 12.0, p = 0.881, Figure 2). If a bat never acquired the novel foraging task, we assigned it an acquisition score of 100 trials; thus, results are conservative measures of task acquisition.

In addition to demonstrating a profound potential for cultural transmission of acoustic-cue associations used in foraging, our results provide evidence as to how such associations might originate in the wild. Most of the bats in the trial-and-error group and the social-facilitation group never learned the novel association between prey cue and prey quality. In each of these groups, one of five bats learned the novel association after more than 80 trials (in the social-facilitation group, this individual reached criterion at 84 trials, and in the trial-and-error group it did so at 81 trials). Thus, although it's rare, bats will inspect calls of poisonous species on their own. This exploratory behavior could enable bats to encounter and track novel sources of prey and could account for the origin of novel associations between prey cue and prey quality in the wild. Such behavior could thus provide a starting point for the rapid cultural transmission that we show here for foraging information among bats.

In other taxa it has been suggested that if mistakes are not costly, it is advantageous for animals to periodically sample their environment. Buchler [8] suggested that wandering shrews (*Sorex vagrans*) make “intentional errors,” even when they know where profitable food patches are located, in order to update their knowledge of their surroundings. Likewise, great tits (*Parus major*)

have been shown to sample a variety of prey species, even when they have a profitable search image for an abundant prey type [9]. In lowland Neotropical rainforests, there can be extreme fluctuations in the abundance of available prey [10]. In the rainy season, frogs call conspicuously, but in the dry season, frogs are harder to find, and *T. cirrhosus* likely has to rely more heavily on non-anuran prey. It is possible that *T. cirrhosus* uses exploratory behavior in combination with social learning to track local and seasonal changes in prey abundance. Because *T. cirrhosus* uses many sensory modalities to assess its prey (e.g., prey-emitted acoustic cues, echolocation cues, and chemical cues), it is likely that a mistake at one level of prey assessment would be corrected at another level. As such, mistakes should not be costly, and behavioral flexibility should be advantageous.

Johnston and Fenton [11] found that pallid bats (*Antrozous pallidus*) vary tremendously in their feeding habits, both between and within populations. Indeed, variation seems to be the rule in many species of bat (e.g., [12, 13]). Dietary studies have shown that *T. cirrhosus* preys on a wide variety of prey items, including frogs, insects, fruit, smaller species of bats, and even birds [14–16], with insects composing the largest component of the diet. No seasonal differences in prey consumption were found in analysis of *T. cirrhosus* stomach contents in Brazil, although this could be due to differences in breeding phenology of frogs present in the areas sampled [14]. Further investigation is necessary for determining whether dietary patterns and foraging preferences vary with season and whether this can be linked to learning within social groups.

Our results clearly demonstrate that if one bat forms a novel acoustic association, in this case evaluating a toad call as a signal of palatable prey, then the association can spread rapidly from bat to bat through cultural transmission. All that is required is that bats observe one another feeding in nature.

T. cirrhosus bats are social. They roost in groups of four to 50 or more individuals [17]. Multiple bats can forage simultaneously at a frog chorus [1, 18], and individuals are often captured together in the same mist net at a foraging site (R.A.P. and M.J.R., unpublished data). Thus, in addition to roosting together, *T. cirrhosus* individuals are known to congregate at feeding sites, thus enabling the observation of foraging conspecifics.

Many species of bat have social structures and foraging habits that should facilitate social learning [19]. Bats are long-lived animals, they tend to form stable groups, and they often feed on temporally and spatially fluctuating resources; thus, cultural transmission of foraging information should increase foraging success [19, 20]. Several studies have shown that bats attend to the foraging behaviors of conspecifics. Many species of

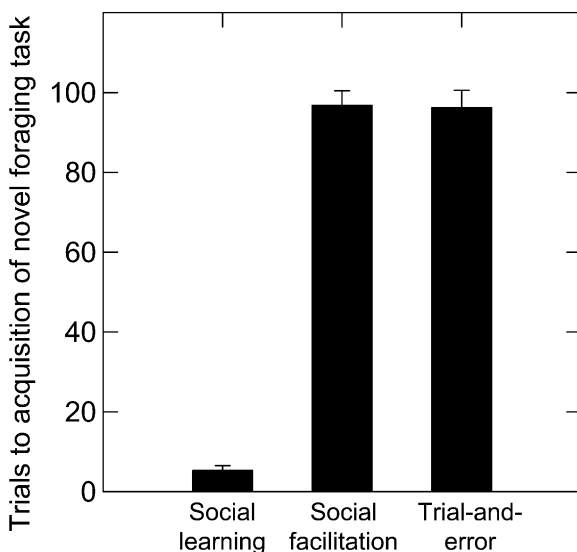


Figure 2. Mean Rates of Acquisition, ± SEM, of the Novel Foraging Task for the Three Learning Groups

insectivorous bats produce loud echolocation calls with distinctive terminal phases as they approach and capture prey. Other individuals eavesdrop on these conspicuous signals and use them to detect aggregations of prey [21, 22]. Likewise, the screech calls of greater spear-nosed bats, *Phyllostomus hastatus*, attract group mates to foraging patches, such as concentrations of flowering balsa [23]. Studies with short-tailed fruit bats, *Carollia perspicillata*, suggest that social learning about temporally fluctuating food resources may even take place at the roost; bats have been shown to use olfactory cues associated with returning roost mates to shape their foraging preferences [20]. These factors suggest that social learning may be common in bats; however, only a handful of studies have demonstrated that bats indeed learn socially about foraging [20, 24–26].

Recent studies have investigated the role of matrilineal kin groups in bat roosting and foraging behavior. Although Kerth et al. [27] found evidence for information transfer about roost sites in Bechstein's bats, *Myotis bechsteinii*, they found no evidence for information transfer about feeding sites. In both the Kerth et al. study and a study of greater horseshoe bats (*Rhinolophus ferrumequinum*), however, radiotracking data demonstrate that mothers and their daughters shared foraging grounds, sometimes for years [27, 28]. Thus, the vertical transfer of foraging-site location from mother to pup could be playing a large role in the foraging dynamics of these bat communities. Although the learning we document in our study is likely entirely opportunistic (the result of one bat eavesdropping on the successful foraging behavior of another), the study of social learning in highly related groups, and especially in mother-pup pairs, should prove an interesting area for further research.

Our study is not designed to distinguish among the mechanisms of social learning [29–32]; however, it is likely that these bats are learning by either stimulus enhancement or observational conditioning. In stimulus enhancement the activity of the tutor draws the observer's attention to the test stimulus [31, 33]—in our experiment, to the toad calls. The observer then forms an association between the stimulus and the reward via individual, trial-and-error learning. Because we altered the speaker location for each trial, we can rule out the possibility that the bats are learning to associate a food reward with a particular spatial location (local enhancement).

In observational conditioning, a type of higher-order conditioning, the observer associates the stimulus with the outcome experienced by the tutor and thus responds more readily to the stimulus itself [31, 34]. In our social-learning treatment, the test bat did not initially attend to the toad calls or to the flight of the tutor bat. In the initial trials, the test bat typically would commence responding with ear motions and head orientation only once the tutor began to consume the food reward, and only in later trials did the test bat respond to the test stimulus. These observations suggest that the sensory cues associated with food consumption by a nearby bat may serve to trigger attention and thus expedite the acquisition of novel foraging associations.

Once the attention of the test bat was elicited, a number of sensory cues could have been involved in the test bat's observation of the tutor. Our experiments were

conducted under low-light conditions, such that visual observation was possible. As *T. cirrhosus* approaches a target, the rate of its echolocation calls increases [35]; thus, the test bat could have used the patterns of the tutor's echolocation calls to follow its behavior. It could also have tracked the movements of the tutor bat with its own echolocation calls, and it could have passively listened to the crashing noise produced when the tutor bat landed on the screen. Further investigation is necessary to determine both the learning mechanisms and the sensory cues involved in this social interaction.

The flexibility, exploratory behavior, and social learning we document in this study endow the bats with the potential to respond rapidly to changes in prey conditions. With the catastrophic and worldwide decline of amphibians [36–38], their predators' ability to track such changes becomes increasingly critical. Rather than falling into ecological traps, unable to quickly alter previously adaptive behavior [39], *T. cirrhosus* should be able to respond quickly to changes in the prey community, the extinction of preferred prey items, and the introduction of novel prey species.

Experimental Procedures

Experiments were conducted at the Smithsonian Tropical Research Institute field station on Barro Colorado Island (BCI), Panama, from February to June 2004 and 2005. We captured the bats in mist nets and tested them in a 4.5 m × 4.5 m × 2.5 m outdoor flight cage. We illuminated the flight cage with a 25 watt red light bulb to facilitate our observations of the bats. This light level was within the range of illuminations in which the bats forage. We used a Sony NightShot DCR-TRV340 camera equipped with a Sony HVL-IRH2 infrared light to record all initial and final tests, all social learning trials, and a subset of the social-facilitation and trial-and-error learning trials. Each bat was marked with a passive integrated transponder (PIT tag) and released at its site of capture after testing. All experiments were licensed by the Smithsonian Tropical Research Institute and the University of Texas at Austin (IACUC #04113002).

Stimulus Presentation

We broadcast calls of *B. marinus* from a Dell Inspiron 8100 computer, a SA-150 Realistic amplifier, and 40-1040 Radio Shack speakers. To approximate the natural call intensity of *B. marinus* in the wild, we broadcast the calls at an amplitude of 75 dB SPL (re. 20 μP) measured at a distance of 1 m from the speaker. Most of the energy in *B. marinus* calls falls between 548 and 708 Hz; the frequency response of these speakers is flat for these frequencies. To ensure that the bats responded to the acoustic stimulus broadcast and not to the speaker itself, we concealed one to five speakers beneath a 1.5 m × 1.5 m screen covered with leaf litter and randomly repositioned the speakers between trials. To ensure that the bats were responding to the toad calls per se and not to other noises associated with the speaker, in a subset of the trials we turned on one of the control speakers and broadcast a sound file of silence. The bats never approached control speakers. Toad calls were broadcast for 60 s or until the test bat landed on the speaker, whichever came first. Trials were conducted in approximately 10 to 15 min intervals with a maximum of 20 trials per night.

Food Rewards and Motivation Levels

Because frogs are protected on BCI, small bait fish were purchased, frozen, thawed, and used as food rewards for the learning trials. The bats readily consumed the fish. To ensure that the bats were not responding to extraneous cues associated with the rewards, in all learning trials we placed multiple rewards in random locations on the screen. Bats only approached food rewards placed on active speakers.

T. cirrhosus picks up its prey in its mouth and flies with it to a nearby perch to consume it. *T. cirrhosus* generally carries only one prey item at a time. We placed many pieces of fish on the active speaker so that if both the tutor and the test bat landed on the speaker in a given trial, each bat would receive a food reward. We closely monitored the bats' food intake to ensure high motivation levels, and trials were conducted only when bats were motivated to feed.

Between trials, we periodically broadcast a probe stimulus known to elicit response in *T. cirrhosus* (the calls of a preferred prey species: either a complex túngara frog call or a chorus of túngara frog calls [1, 40]). If the test bat did not respond to the probe stimulus, we could infer that a lack of response to the toad calls could have been due to factors other than the salience of the test stimuli (i.e., handling stress, fear of new environment, satiation). Bats always responded readily to the probe stimuli in all probe tests.

Summary of Trials

1. Initial Trials

To determine its baseline response to toad calls, we first tested each bat alone, without rewards on the speaker. Toad calls were broadcast for 60 s or until the bat approached and landed on the speaker, whichever came first. Three initial tests were conducted for each bat.

2. Learning Trials

Three types of learning trials were conducted: (a) social learning, (b) social facilitation, and (c) trial and error. Learning trials were conducted until criterion (flying to and landing on the speaker in three consecutive trials) had been reached or until 100 trials had been conducted, whichever came first. Food rewards were placed on the speaker in all learning trials.

3. Final Trials

After learning trials, we removed the tutor bat and conducted three final trials with the test bat alone. The protocol for final tests was identical to initial tests. Final test results mirrored criterion results: all bats that reached criterion in the learning trials responded to toad calls by flying to and landing on the speaker in all three final trials. No bat that failed to reach criterion in the learning trials responded in the final trials.

Supplemental Data

One supplemental figure is available with this article online at <http://www.current-biology.com/cgi/content/full/16/12/1201/DC1/>.

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References

1. Tuttle, M.D., and Ryan, M.J. (1981). Bat predation and the evolution of frog vocalizations in the Neotropics. *Science* 214, 677–678.
2. Page, R.A., and Ryan, M.J. (2005). Flexibility in assessment of prey cues: Frog-eating bats and frog calls. *Proc. R. Soc. Lond. Biol. Sci.* 272, 841–847.
3. Lefebvre, L., and Giraldeau, L.-A. (1996). Is social learning an adaptive specialization? In *Social Learning in Animals: The Roots of Culture*, C.M. Heyes and B.G. Galef, Jr., eds. (San Diego: Academic Press), pp. 107–128.
4. Galef, B.G., Jr. (1995). Why behaviour patterns that animals learn socially are locally adaptive. *Anim. Behav.* 49, 1325–1334.
5. Galef, B.G., Jr., and Giraldeau, L.-A. (2001). Social influences on foraging in vertebrates: causal mechanisms and adaptive functions. *Anim. Behav.* 61, 3–15.
6. Terrace, H.S. (1963). Discrimination learning with and without “errors”. *J. Exp. Anal. Behav.* 6, 1–27.
7. Zajonc, R.B. (1965). Social facilitation. *Science* 149, 269–274.
8. Buchler, E.R. (1976). The use of echolocation by the wandering shrew (*Sorex vagrans*). *Anim. Behav.* 24, 858–873.
9. Tinbergen, L. (1960). The natural control of insects in pinewoods. I. Factors influencing the intensity of predation by some birds. *Archs. Neerl. Zool.* 13, 266–336.
10. E.G. Leigh, Jr., A.S. Rand, and D.M. Windsor, eds. (1982). *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes* (Washington, DC: Smithsonian Institution Press).
11. Johnston, D.S., and Fenton, M.B. (2001). Individual and population-level variability in diets of pallid bats (*Antrozous pallidus*). *J. Mammal.* 82, 362–373.
12. Norberg, U.M., and Fenton, M.B. (1988). Carnivorous bats? *Biol. J. Linn. Soc.* 33, 383–394.
13. Fenton, M.B., Swanepoel, C.M., Brigham, R.M., Cebek, J., and Hickey, M.B.C. (1990). Foraging behavior and prey selection by large slit-faced bats (*Nycteris grandis*; Chiroptera: Nycteridae). *Biotropica* 22, 2–8.
14. Bonato, V., Faure, K.G., and Uieda, W. (2004). Food habits of bats of subfamily Vampyrinae in Brazil. *J. Mammal.* 85, 708–713.
15. Bonato, V., and Facure, K.G. (2000). Bat predation by the fringe-lipped bat, *Trachops cirrhosus* (Phyllostomidae, Chiroptera). *Mammalia* 64, 241–243.
16. Giannini, N.P., and Kalko, E.K.V. (2004). Trophic structure in a large assemblage of phyllostomid bats in Panama. *Oikos* 105, 209–220.
17. Cramer, M.J., Willig, M.R., and Jones, C. (2001). *Trachops cirrhosus*. *Mamm. Species* 656, 1–6.
18. Ryan, M.J., Tuttle, M.D., and Taft, L.K. (1981). The costs and benefits of frog chorusing behavior. *Behav. Ecol. Sociobiol.* 8, 273–278.
19. Wilkinson, G.S., and Boughman, J.W. (1999). Social influences on foraging in bats. In *Mammalian Social Learning: Comparative and Ecological Perspectives*, H.O. Box and K.R. Gibson, eds. (Cambridge, UK: Cambridge University Press), pp. 188–204.
20. Ratcliffe, J.M., and ter Hofstede, H.M. (2005). Roosts as information centres: Social learning of food preferences in bats. *Biol. Lett.* 1, 72–74.
21. Barclay, R.M.R. (1982). Interindividual use of echolocation calls: Eavesdropping by bats. *Behav. Ecol. Sociobiol.* 10, 271–275.
22. Balcombe, J.P., and Fenton, M.B. (1988). Eavesdropping by bats: The influence of echolocation call design and foraging strategy. *Ethology* 79, 158–166.
23. Wilkinson, G.S., and Boughman, J.W. (1998). Social calls coordinate foraging in greater spear-nosed bats. *Anim. Behav.* 55, 337–350.
24. Gaudet, C.L., and Fenton, M.B. (1984). Observational learning in three species of insectivorous bats (Chiroptera). *Anim. Behav.* 32, 385–388.
25. Wilkinson, G.S. (1992). Information transfer at evening bat colonies. *Anim. Behav.* 44, 501–518.
26. Wilkinson, G.S. (1995). Information transfer in bats. *Symp. Zool. Soc. Lond.* 67, 345–360.
27. Kerth, G., Wagner, M., and König, B. (2001). Roosting together, foraging apart: information transfer about food is unlikely to explain sociality in female Bechstein's bats (*Myotis bechsteinii*). *Behav. Ecol. Sociobiol.* 50, 283–291.
28. Rossiter, S.J., Jones, G., Ransome, R.D., and Barratt, E.M. (2002). Relatedness structure and kin-based foraging in the greater horseshoe bat (*Rhinolophus ferrumequinum*). *Behav. Ecol. Sociobiol.* 51, 510–518.
29. Zentall, T.R. (1996). An analysis of imitative learning in animals. In *Social Learning in Animals: The Roots of Culture*, C.M. Heyes and B.G. Galef, Jr., eds. (New York: Academic Press), pp. 221–243.

30. Whiten, A., and Ham, R. (1992). On the nature and evolution of imitation in the animal kingdom: Reappraisal of a century of research. In *Advances in the Study of Behavior*, P.J.B. Slater, C. Rosenblatt, C. Beer, and M. Milinski, eds. (New York: Academic Press), pp. 239–283.
31. Heyes, C.M. (1994). Social learning in animals: Categories and mechanisms. *Biol. Rev.* 69, 207–231.
32. Galef, B.G., Jr. (1988). Imitation in animals: History, definition, and interpretation of data from the psychological laboratory. In *Social Learning: Psychological and Biological Perspectives*, T.R. Zentall and B.J. Galef, Jr., eds. (Hillsdale, NJ: Erlbaum), pp. 3–28.
33. Fritz, J., Bisenberger, A., and Kotrschal, K. (2000). Stimulus enhancement in greylag geese: Socially mediated learning of an operant task. *Anim. Behav.* 59, 1119–1125.
34. Mineka, S., Davidson, M., Cook, M., and Keir, R. (1984). Observational conditioning of snake fear in rhesus monkeys. *J. Abnorm. Psychol.* 93, 355–372.
35. Barclay, R.M.R., Fenton, M.B., Tuttle, M.D., and Ryan, M.J. (1981). Echolocation calls produced by *Trachops cirrhosus* (Chiroptera: Phyllostomatidae) while hunting for frogs. *Can. J. Zool.* 59, 750–753.
36. Stuart, S.N., Chanson, J.S., Cox, N.A., Young, B.E., Rodrigues, A.S.L., Fischman, D.L., and Waller, R.W. (2004). Status and trends of amphibian declines and extinctions worldwide. *Science* 306, 1783–1786.
37. Lips, K.R., Brem, F., Brenes, R., Reeve, J.D., Alford, R.A., Voyles, J., Carey, C., Livo, L., Pessier, A.P., and Collins, J.P. (2006). Emerging infectious disease and the loss of biodiversity in a Neotropical amphibian community. *Proc. Natl. Acad. Sci. USA* 103, 3165–3170.
38. Pounds, J.A., Bustamante, M.R., Coloma, L.A., Consuegra, J.A., Fogden, M.P., Foster, P.N., La Marca, E., Masters, K.L., Merino-Viteri, A., Puschendorf, R., et al. (2006). Widespread amphibian extinctions from epidemic disease driven by global warming. *Nature* 439, 161–167.
39. Schlaepfer, M.A., Runge, M.C., and Sherman, P.W. (2002). Ecological and evolutionary traps. *Trends Ecol. Evol.* 17, 474–480.
40. Ryan, M.J., Tuttle, M.D., and Rand, A.S. (1982). Bat predation and sexual advertisement in a Neotropical anuran. *Am. Nat.* 119, 136–139.