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Animal Behavior: Who Will Croak Next?

A recent study with the predatory bat *Trachops cirrhosus* has shown the importance for this species of social learning about novel prey using auditory, rather than visual or olfactory, cues.

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Observations of social learning of foraging behaviors in non-human animals have long fascinated naturalists. Among the most celebrated documentations of innovation and social learning in animals involve washing of sweet potatoes and wheat by free-ranging Japanese macaques (*Macaca fuscata*) and opening milk bottles by titmice (*Parus* spp.). These beneficial behaviors were first observed in one or a small number of individuals, but then they spread through populations [1]. These and other studies have inspired careful experimental designs to determine the sensory cues and cognitive mechanisms underlying innovation and social learning in non-human animals. Visual and sometimes olfactory cues have been shown to provide the basis for information transfer between individuals in many species [2].

In this issue of *Current Biology*, Page and Ryan [3] report how fringe-lipped bats, *Trachops cirrhosus* (Figure 1), learn from one another by attending to prey-generated acoustic cues and bat feeding sounds (sounds of lip smacking and chewing). Earlier, Page and Ryan [4] had shown that fringe-lipped bats make and reverse novel cue–consequence associations between the mating songs of anurans (frogs and toads) and their relative profitability as prey. Their new work used this behavioral flexibility in cue–consequence association as a vehicle for training some bats — 'tutors' — to approach speakers playing mating calls of adult male cane toads (*Bufo marinus*) and then receive a nutritious reward. *Bufo marinus* is poisonous and adults are much too large for the bats to eat.

Bats inexperienced with the toad call–profitable resource association were allowed to observe tutors taking pieces of fish placed on a horizontal screen above microphones broadcasting

Figure 1. Fringe-lipped bats are best known for preying on frogs but also eat a variety of other animal prey. Fringe-lipped bats use male frog calls to locate and identify potential prey. Page and Ryan [3] have demonstrated that these bats learn to associate toad calls with food rewards, behavior that is learned through observation of conspecifics. (Photo courtesy of Sandra Peters.)

Bufo marinus calls. Ten bats quickly learned (in about five trials on average) from their tutor to make the association. In turn, they served as tutors for the next inexperienced bat in the 'chain'.

This social learning was both rapid and profound. Bats introduced to tutors later in the chain learned the novel prey cue–prey quality association as quickly as bats earlier in the chain. Bats in a trial-and-error learning group — tested without tutors — as well as bats in a social facilitation group — two inexperienced bats introduced together — seldom learned to associate toad calls with profitable prey in fewer than 100 trials.

Both toad calls and the bats' eating sounds appear important for social transmission of useful information about a novel, beneficial prey item. It also is possible that echolocation calls produced before capture may attract the attention of other bats [5] and have a promoting effect, playing a role in social learning of predatory behavior by fringe-lipped bats. Three different cues — echolocation calls, mating calls and chewing sounds — from two distinct sources — bats and frogs — are received by bats' auditory systems and may represent signals that function in a staged and at times overlapping way. As Page and Ryan [3] themselves point out, their study does not attempt to characterize the relative importance of these or other potential sensory cues for making novel prey cue–prey quality associations.

Page's and Ryan's work [3,4] suggests that bats could prove to be excellent models for future studies designed to determine the relative roles of each cue and the cognitive mechanisms underlying task acquisition and future decision-making processes. The diversity of bats (>1100 species) makes them attractive as subjects. While many species echolocate and attend to acoustic cues from prey, others do not. While all species are relatively small and long-lived, some are solitary and others form cohesive social units.

For individual learning, we are particularly interested in finding out whether the fringe-lipped bat's remarkable behavioral flexibility in diet selection is maintained during taste–toxicity associations. In bats and other animals, such associations are typically made in a single-trial, are persistent and not easily reversed [6].

The bats that Page and Ryan [3] studied were wild-caught adults, so their histories with the calls of the cane toads are not known. There are at least three possible explanations for each fringe-lipped bat's initial lack of response to calls of cane toads: first, the bat had never investigated the calls of cane toads in the wild; second, the bat had previous aversive experiences (for example, from noxious chemical cues on the toad's skin); or third, the bat had investigated toad calls and identified adult male toads as being too large to successfully handle and consume. Regardless, Page and Ryan [3] have shown that naturally occurring signals, not previously associated with a beneficial reward, are investigated by individual bats from time to time under ecologically relevant conditions. Once formed, novel positive associations between song and prey can be readily and rapidly transmitted via social learning.

Fringe-lipped bats use an eavesdropping hunting strategy, listening for mating calls to detect and localize male frogs and toads [7]. Page's and Ryan's [3] results reveal that these predators can eavesdrop on bats hunting nearby and learn of previously unexploited anuran species and perhaps other nocturnal, actively sound-producing animals, such as crickets and katydids. Their findings illuminate earlier results demonstrating that fringe-lipped bats eat a range of prey, not just some anurans [8,9]. Their results also provide new interpretations of variations in bat diet that could result from social learning (for example, [10]).

Page and Ryan's [3] elegant study provides valuable insight into how behaviorally flexible predators could deal with changing prey communities. Changes in communities could reflect variations over season or time, but they also can result from anthropogenic extinctions and introductions. The authors have opened a new avenue for research into social transmission of prey preference from mothers to pups in bats and provide an experimental template for investigations in to the possibility of socially induced aversions to acoustic cues produced by noxious, or otherwise unprofitable, prey.

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