

# Chapter 11

## Overcoming Sensory Uncertainty: Factors Affecting Foraging Decisions in Frog-Eating Bats

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**Abstract** Predators forage in complex environments where they must make fast, high-stakes decisions. Foraging decisions are influenced by biases in sensory perception and cognitive processing, learned and remembered information, and environmental factors such as prey availability. In this chapter, we discuss some of the factors that influence decision-making in a neotropical predatory bat species, the fringe-lipped bat, *Trachops cirrhosus*. This bat hunts frogs and insects by eavesdropping on prey-produced sounds, but its foraging decisions are also influenced by other sources of information, including echoacoustic and gustatory cues. *T. cirrhosus* quickly learns novel associations between prey cue and quality, can use social information acquired from conspecifics, and forms long-term memories of prey sounds. Research on perception and cognition in this predatory bat, all conducted with wild or wild-caught and temporarily housed individuals, has made this species one of the most well-understood, non-model systems for predator decision-making. Yet there is still much that remains unknown about how and why these predators make the foraging decisions they do.

### 11.1 Introduction

Optimal foraging theory predicts that individuals make foraging decisions that maximize fitness (Emlen 1966; MacArthur and Pianka 1966). But in nature, uncertainties abound, and for each foraging decision, an animal must make the best of imperfect information. Foraging animals have access to multiple sources of

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information, each with costs and benefits. Prey cues can be obscured by a cacophony of background information assaulting multiple sensory modalities. Predators may also vary in their experience with different prey species and may have incomplete knowledge about which prey are palatable and which are poisonous, which are easy to capture and subdue, and which may turn the tables and attack the predator. Foraging mistakes at the least incur wasted resources of time or energy. Such mistakes can also have much greater costs, such as when errors in prey assessment result in predators mistakenly consuming toxic prey. Movement through the environment, especially the conspicuous movement involved in prey pursuit and capture, not only can give prey warning of impending attack but also can put captors in the risky position of alerting their own predators to their presence and potentially becoming prey themselves. Predator decision-making encompasses a wide array of risks, but without taking these risks, and doing so efficiently, predators lack the calories they need. The decision of when, where, and what to hunt is critical to predator survival.

The investigation of predator decision-making consists of intertwined lines of research investigating sensation, perception, and cognition. Studies of sensation and perception are concerned with identifying the sensory inputs to which a predator attends and how a predator's sensory system has evolved to increase sensitivity to certain prey cues over others. In studies of cognition, questions focus on how a predator shifts its attention between sensory cues, how it integrates and utilizes input from multiple sensory modalities, how long predators remember learned prey cues, and how these factors vary with fluctuations in social and environmental conditions. Both the sensory and cognitive components of predator decision-making impose selective consequences on predator foraging success and on prey survival.

### ***11.1.1 Sensation, Perception, and Cognition in Predator Decision-Making***

Predators use multiple sensory modalities to detect and localize prey. Sensory systems can influence foraging choices through both their separate sensitivity and tuning and through their perceptual integration. Sensory systems of animals are often restricted or tuned to be most responsive to a particular subset of the range of available stimuli (Chap. 2). A means for prey signals to be less detectable to predators is to be outside the restricted range of a predator's sensory system (Håstad et al. 2005; Stuart-Fox et al. 2008). Tuning of sensory systems therefore has important consequences for prey detection. Limitations in prey detection in one sensory system can be alleviated by the use of an additional sensory modality. The use of multiple sources of information can improve the accuracy and speed of decision-making (Rowe 1999; Roberts et al. 2007; Ward and Mehner 2010) and may be particularly beneficial in complex or uncertain environments (Rhebergen

et al. 2015; Chap. 5). Multimodal stimuli can also be learned faster than stimuli in only a single sensory modality (Rowe 1999). To understand predator response to prey cues, it is, therefore, important to examine not only the response of different sensory systems to particular prey cues but additionally how these sources of sensory information are perceptually integrated.

Learning and memory also play important roles in predator decision-making. Learning abilities can be subject to natural selection due to environmental variation (Mettke-Hofmann 2014), foraging niche (Clarín et al. 2013), predation pressure (Brown and Braithwaite 2005), and social complexity (Byrne and Bates 2007). Studying the evolution of cognition in the field is a particularly challenging research area that is currently of great interest in behavioral ecology (Morand-Ferron and Quinn 2015). The majority of the research on foraging-related cognition in non-model systems has focused on birds, from tool use in New Caledonian crows (*Corvus moneduloides*, Hunt and Gray 2004) to food caching in black-capped chickadees (*Poecile atricapillus*, Pravosudov and Clayton 2002) and social learning in great tits (*Parus major*, Aplin et al. 2015). Learning enables predators to be flexible in their responses to prey cues to take advantage of temporal and geographic variation in prey availability.

### 11.1.2 Study System

Our system for examining the perceptual and cognitive factors influencing decision-making is the fringe-lipped bat, *Trachops cirrhosus*. *T. cirrhosus* is in the family Phyllostomidae, the leaf-nosed bats, and is found in tropical lowland forests from southern Mexico to Brazil (Cramer et al. 2001). It is a mid-sized tropical bat (~30 g, ~40-cm wingspan, Fig. 11.1) that feeds on a wide variety of prey species, including insects, frogs, lizards, and other small vertebrates (Gardner 1977; Pine and Anderson 1979; Kalko et al. 1996; Bonato and Facure 2000; Bonato et al. 2004; Rodrigues et al. 2004; Giannini and Kalko 2005). *T. cirrhosus* roosts in small mixed-sex groups in hollow trees (often cashews, *Anacardium excelsum*, Kalko et al. 1999), tunnels, caves, and culverts (Jones 1966; Handley 1976). Individuals forage in overlapping areas that average around 60 hectares (Jones et al. *in review*). In 1977, Merlin Tuttle was mist netting for bats at the Smithsonian Tropical Research Institute on Barro Colorado Island (BCI) in Panama and captured a *T. cirrhosus* holding a túngara frog in its mouth (Tuttle 2015). He began to investigate, comparing capture rates of *T. cirrhosus* in mist nets with and without speakers broadcasting túngara frog calls and presenting different acoustic stimuli in a flight cage. In 1980, he approached then graduate student Michael J. Ryan, who, under the mentorship of A. Stanley Rand, was studying the mating calls of túngara frogs on BCI. Together they decided to examine how *T. cirrhosus* hunts frogs. When they discovered that *T. cirrhosus* will attack speakers broadcasting túngara frog calls (Tuttle and Ryan 1981), they initiated what would become now a four-



**Fig. 11.1** The fringe-lipped bat (*Trachops cirrhosus*) preys on frogs by homing in on their sexual advertisement calls. In these images, a bat approaches and consumes a calling male túngara frog (*Physalaemus pustulosus*), one of its preferred prey species. Photos courtesy Lars Hedin (*upper left*) and Alexander T. Baugh (*bottom left and right*)

decade-long study of sensation (Sect. 11.2), perception (Sect. 11.2), and cognition (Sect. 11.3) in this extraordinary bat species (Page et al. 2014).

## 11.2 Sensation and Perception

In the rainforest at night, the senses are assaulted by a myriad of diverse stimuli. Frogs and insects call to attract mates, sometimes singly, sometimes in deafening choruses. Night-blooming flowers waft intense, pungent odors. And for those who can hear ultrasound, bat and insect calls bombard the soundscape. How does a predator make sense of this cacophony and, from it, target individual prey? In a problem akin to a human attempting to attend to a single string of conversation in the boisterous confusion of a loud cocktail party (Cherry 1953; Bee and Micheyl 2008), an eavesdropping predator relies on multiple streams of sensory information to perceive and target a single prey item amidst the myriad sensory cues present in a rainforest at night.

In this section on sensation and perception, we discuss the multiple sensory inputs used by *T. cirrhosus* in their hunt for frogs. *T. cirrhosus* is now well known for locating frogs by eavesdropping on frog calls. In the bat literature, this type of prey localization is referred to as “passive listening” because it relies on prey-produced cues. Echolocation, in contrast, is often referred to as “active listening”

because it is a product of bat-produced echolocation calls (Schnitzler et al. 2003). To evaluate food, many species of bats use both passive and active listening (Russo et al. 2007), as well as vision (Bell 1985), olfaction (Mikich et al. 2003), and gustation (Hristov and Conner 2005). Bats therefore have access to multiple sensory systems for perceiving potential prey. The research detailed in this section has investigated factors influencing bat responses to prey in these different sensory systems, and then how they are integrated as bats make a decision to attack.

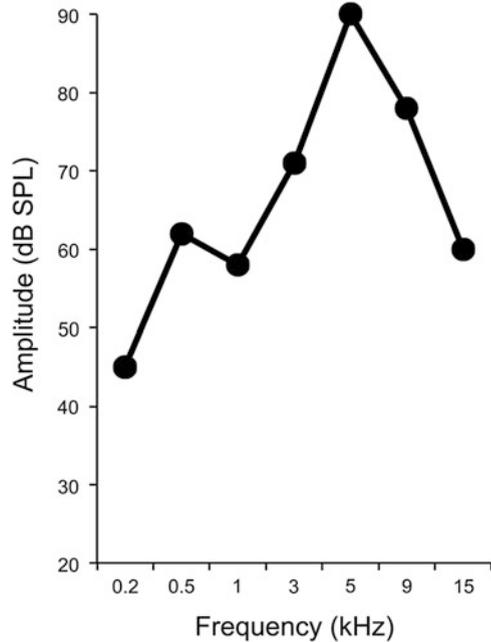
### 11.2.1 *Passive Listening*

Passive listening is believed to be common in bats that hunt in cluttered environments (such as close to the ground or vegetation), because clutter makes locating stationary prey by echolocation nearly impossible due to the effects of backward and forward masking (Neuweiler 1989; Schnitzler and Kalko 2001; Siemers and Schnitzler 2004). Other passive listening bats attend to the broadband rustling sounds of prey moving through leaf litter (Goerlitz and Siemers 2007) or the high-frequency calls of insects such as katydids (Tuttle et al. 1985; Jones et al. 2011; Falk et al. 2015). These prey-generated cues often have high-frequency components that fall in the range of the bats' hearing, which is centered on the ultrasonic frequencies of the bats' own echolocation calls.

The demonstration by Tuttle and Ryan (1981) that *T. cirrhosus* locates frogs by their calls was such an extraordinary discovery, in part, because bats were not believed to be able to hear the low frequencies (< 5 kHz) of frog calls. It was soon after discovered that unlike most other bats, *T. cirrhosus* has a peak of auditory sensitivity below 5 kHz, the frequency range of the calls of many frog species (Fig. 11.2; Ryan et al. 1983). This additional peak in sensitivity is reflected in the neuroanatomy of this bat's ear. *T. cirrhosus* has the highest number of cochlear neurons reported for any mammal and has an additional peak of neural cochlear density not reported for any other bat species (Bruns et al. 1989). This additional peak of neural density is found in the apical portion of the cochlea (Bruns et al. 1989), the portion of the cochlea sensitive to low-frequency sounds (von Békésy 1960), suggesting auditory specialization for low-frequency sounds, such as frog calls.

Although *T. cirrhosus* eavesdrops on the calls of a number of frog (Tuttle and Ryan 1981) and katydid (Falk et al. 2015) species, the majority of work has examined the relationship between *T. cirrhosus* and the túngara frog, *Physalaemus* (= *Engystomops*) *pustulosus*. The túngara frog is a small (approximately 2 g) frog in the family Leptodactylidae that occurs throughout Middle America (Fig. 11.1). Male túngara frogs can produce two types of call: simple and complex (Fig. 11.3; Chap. 4). Both simple and complex calls contain a frequency modulated sweep or "whine," consisting of a fundamental frequency that sweeps from about 0.9 kHz to 0.4 kHz and is about 300 ms in duration. The whine has several harmonics, with an average dominant frequency of about 700 Hz. Simple túngara frog calls consist of a

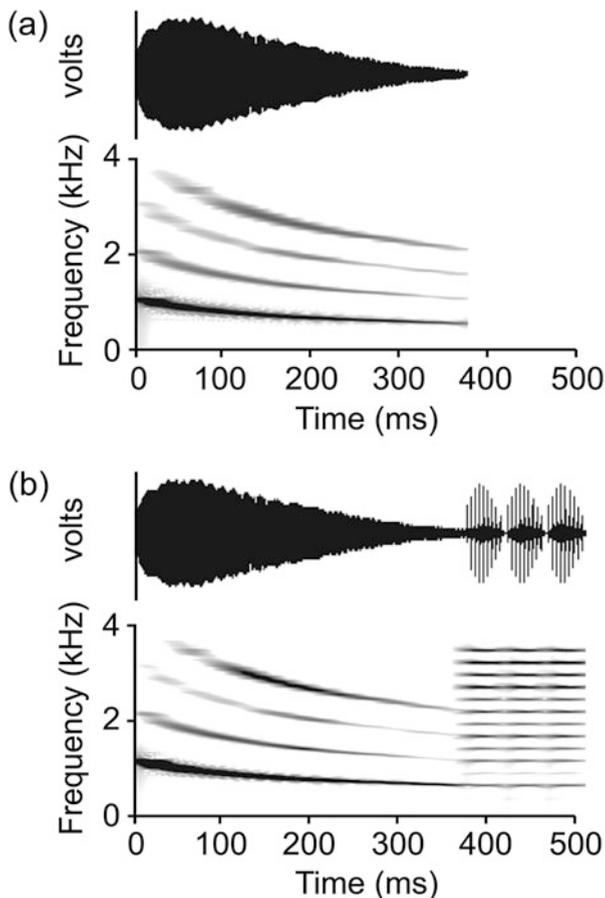
**Fig. 11.2** Behavioral audiogram of a fringe-lipped bat (*Trachops cirrhosus*). Points depict the threshold amplitudes required to elicit an ear-twitching response from a perched bat in response to pure tones. Relatively lower threshold amplitudes represent greater auditory sensitivity. Note the increase in auditory sensitivity as frequencies drop below 5 kHz. Modified from Ryan et al. (1983) and used with permission



whine alone. Complex calls consist of the whine plus one to seven broadband suffixes termed “chucks.” Chucks have a dominant frequency of about 2500 Hz and a duration of 35 ms. Except in very rare cases (Ryan et al. 2015), chucks are never produced alone; they are always produced right after a whine. Both female túngara frogs (Rand and Ryan 1981; Gridi-Papp et al. 2006) and frog-eating bats (Ryan et al. 1982; Fugère et al. 2015; Akre et al. 2011) strongly prefer complex calls to simple ones, thus exerting conflicting selective pressures on the calling male.

When a group of túngara frogs are all calling together, the cacophony is such that to a human listener, it is difficult to distinguish which males are making simple calls and which are making complex calls. Locating an individual male in a loud chorus is a perceptual and cognitive challenge for female frogs (Bee and Micheyl 2008; Bee 2015; Chap. 4) and eavesdropping predators alike. A study by Jones et al. (2013a) investigated how bats respond to the different components of the túngara frog call. In particular, it examined whether bats orient toward one particular component of the call and whether they attend to the order in which the two syllables occur (in nature, chucks always follow whines). This study built off of similar research questions conducted with female túngara frogs (Farris et al. 2002, 2005; Chap. 4). Female túngara frogs strongly prefer complex calls (Gridi-Papp et al. 2006) and will not approach chucks played alone without a whine. However, if a whine is broadcast in the vicinity of a speaker playing a chuck, the females will orient toward the chuck, even with quite large spatial separations between the two call components (up to 135°, Farris et al. 2002). Female túngara frogs therefore appear to require the whine component of the call to initiate phonotaxis, indicating

**Fig. 11.3** Advertisement call of the túngara frog (*Physalaemus pustulosus*). Waveforms (*top*) and spectrograms (*bottom*) of (a) a simple call with no chucks and (b) a complex call with three chucks. Modified from Fugère et al. (2015) and used with permission



auditory grouping of these two call components, but then they preferentially approach the chuck even when it is spatially separated from the whine or broadcast in reversed temporal order such that it proceeds the whine (Farris et al. 2005).

*T. cirrhosus* also exhibits phonotaxis to male túngara frog calls, but bats conduct this behavior under different selective pressures and from a very divergent evolutionary starting point than female túngara frogs. Bats respond dramatically differently to isolated call components. Unlike túngara frogs, bats respond to the chuck component of the call when it is played alone, and they preferentially approach the whine over the chuck when the two components are spatially separated. If the chuck is played before the whine (the reverse of the natural order), bat approaches to the chuck increase, indicating an effect of temporal sequence (Jones et al. 2013a). These differences in responses between female túngara frogs and fringe-lipped bats highlight the different factors that weigh into decisions by these different receivers. For example, bats may be under strong selection to respond to túngara frog calls as quickly as possible so they catch their prey before it stops calling or escapes, as

túngara frogs often do when they detect an approaching bat (Tuttle et al. 1982). A general preference for the first component of the call might increase the speed at which bats can make a decision to attack. The duration of a signal increases its detectability (Campbell 1963), which may explain why bats preferentially approach the whine over the chuck alone. It is important to note, however, that the whine is only preferred over the chuck *alone*. Complex calls (whines plus chucks) are still strongly preferred over simple calls (whines alone; Fugère et al. 2015). Jones et al. (2013a) showed that bats are particularly responsive to the first part of the call (in nature, this is the whine for both simple and complex calls), and bats clearly prefer the whine alone to the chuck alone, perhaps because of its duration or because the whine is a highly recognizable component of the túngara frog call. A given male facultatively makes either the whine alone or whines plus chucks. So why do bats prefer complex calls to simple ones?

Four non-exclusive hypotheses have been investigated for the preference for complex calls in *T. cirrhosus*. The first two hypotheses are based on the idea that complex calls indicate something about the prey. Bats could prefer complex calls because they signify larger males with better body condition, that is, more substantial meals. Field recordings of calling túngara frogs, however, reveal that there is no correlation between túngara frog call complexity and body length, mass, or condition (Bernal et al. 2007). A second possibility is that call complexity is an indicator of male density: complex calls indicate high-density patches of prey. This is indeed the case. The number of male túngara frogs calling within 1 m of a particular frog is correlated both with the proportion of complex calls that a male produces and with the average number of chucks he makes per call (Bernal et al. 2007). Bats may, therefore, preferentially approach complex calls because they are indicators of high prey density.

The next two hypotheses are centered around preference for call complexity as a product of bat sensory and perceptual processing. It has long been hypothesized that males that produce complex calls are easier for bats to localize because the calls are longer in duration (Campbell 1963) or because of the acoustic properties of the chuck. The chuck is short (approximately 35 ms) and has a broadband structure with a fast onset and offset, acoustic properties that should make it easier to localize (Marler 1955) than the whine. Phonotaxis experiments in a flight cage broadcasted túngara frog calls from speakers underneath screens covered in leaf litter (Page and Ryan 2008). When the bats landed on the screen, distance from the landing place to the speaker was compared for simple versus complex calls. Under most conditions, bats showed no difference in localization ability when approaching simple versus complex calls. Bats did localize complex calls better under three conditions: when (1) there was background noise present, (2) the calls were only broadcast before the bats began to approach and then shut off during approach, and (3) when the calls were only broadcast before approach and there were obstacles (hanging wooden dowels) between the perched bat and the speakers. If the calls were broadcast continuously with or without obstacles present, however, there was no improved localization (Page and Ryan 2008). The acoustic properties of the complex call that

improve localization may, therefore, be only a partial explanation for bats' preference for the complex call.

The fourth hypothesis for bat preference for complex calls is that the auditory reception and processing of *T. cirrhosus* may be particularly stimulated by properties of the complex call, producing a perceptual bias for call complexity. A perceptual bias occurs when sensory and cognitive systems are biased (e.g., due to neural or chemical pathways) to be more sensitive to particular stimuli (Endler and Basolo 1998; Frame and Servedio 2012; Ryan and Cummings 2013). An example of perceptual bias is the responsiveness of mammalian auditory and cognitive systems to nonlinear sounds such as screams (Blumstein and Récapet 2009). Three different experiments have examined whether there may be a perceptual bias for complex calls in fringe-lipped bats. First, flight cage experiments presented bats with simple calls modified to contain the acoustic properties of a complex call (longer duration, greater energy, increased amplitude modulation; Fugère et al. 2015). If perceptual bias for acoustic parameters explained the preference for complex calls, then these modified calls should be equally preferred to complex calls and preferred over unmodified whines. The study also included a set of stimuli in which the acoustic parameters were exaggerated beyond those of the complex call, with the hypothesis that these stimuli should be preferred over the complex call. No modified whine was found to be more attractive than the unmodified whine, with the exception of one of the exaggerated calls modified to be as long as a complex call with six chucks (a call that is very uncommon in nature: Bernal et al. 2007; Fugère et al. 2015). This study indicates that it is possible that preference for complex calls is due to a perceptual bias for longer stimuli, but this is in need of further support.

An additional result from Fugère et al. (2015) was that bats strongly preferred the unmodified whine when paired with a modified whine that had most of its call energy in higher frequencies (in the third harmonic: over 2 kHz). Unmodified whines have most of their energy in the fundamental frequency (below 1 kHz). The bats' strong preference for unmodified whines when the alternative consisted of whines with their low frequencies removed makes sense in light of the behavioral audiogram of *T. cirrhosus*. Less sound energy is necessary to evoke a behavioral response in these bats at frequencies below 1 kHz than at frequencies above 2 kHz (Fig. 11.2; Ryan et al. 1983). The modified whines with more energy in these higher frequencies than in the lower frequencies probably sounded quieter to the bats than the unmodified whines did. As frog-eating bats prefer louder signals to quieter ones (Tuttle and Ryan 1981), their preference for unmodified whines over high-frequency modified whines is intuitive to us, as these modified calls, though matched in amplitude, likely sounded fainter to them than the unmodified calls. It is interesting to note that the dominant frequency of the túngara frog's chuck (approximately 2.5 kHz) is higher than the sonic frequencies to which *T. cirrhosus* is most sensitive. Did túngara frogs evolve away from lower-frequency chucks to reduce predation pressure from bats? An interesting avenue of research would be to compare chuck frequencies in populations of túngara frogs that vary in their degree of bat predation, as has been done in other systems, for example, in Trinidadian

guppies that show increased intensity of nuptial coloration in populations under lower predation pressure (Endler 1986). Additionally, it would be interesting to compare the auditory sensitivity of bats across populations that vary in available prey. While this population comparison has not been conducted with auditory sensitivity, the two experiments discussed next did compared behavioral responses to prey calls across populations with different availability of complex calls.

Túngara frogs are not present in Amazonian Ecuador, but their sister species, Peter's dwarf frog, *Physalaemus petersi*, occurs there. As in túngara frogs, these frogs have a two-part call that consists of a frequency-modulated whine (the simple call) that can be facultatively followed by secondary component called a "squawk" (producing a complex call). Curiously, in some populations of *P. petersi*, males produce complex calls, while in other nearby populations, they do not (Boul and Ryan 2004). Trillo et al. (2013) broadcast simple and complex *P. petersi* calls from speakers in the forest and monitored bat approaches with infrared video in two locations in Amazonian Ecuador, one with complex calling *P. petersi* and the other with only simple calling *P. petersi*. Playback experiments demonstrated that bats prefer complex calls in both locations: in the area in which the frogs produce complex calls and in the area in which they produce only simple calls. It is unclear why bats prefer the calls of frogs making squawks in a population where frogs only make simple calls. It is possible that this is evidence for a perceptual bias for call complexity. It could also be that this population of frogs used to make complex calls in the past and the bat preference for complex calls is genetically controlled and is maintained. Studies from Panama show small home ranges for *T. cirrhosus* (Kalko et al. 1999), but no such tracking data is available for the Ecuadorian *T. cirrhosus*. Another possibility is that the bats fly between these frog populations and thus experience both call types. Further study is necessary to resolve these intriguing results.

A second study adds yet another layer to the story. Jones et al. (2014) investigated a population of *T. cirrhosus* at the La Selva Biological Station in Costa Rica, where *Physalaemus* is completely absent. *T. cirrhosus* in this population did not show phonotaxis toward either simple or complex túngara frog calls. The discrepancy between Trillo et al. (2013) and Jones et al. (2014) could have a number of explanations. It is possible that familiarity with simple calls predisposes bats to be more responsive to complex calls, but it is also possible that response to prey calls is genetically determined and diverges between populations that differ in prey availability.

The preference for complex calls in *T. cirrhosus*, therefore, remains a subject of debate. Future studies could fruitfully examine the responses of completely naïve, lab-reared juveniles to simple and complex túngara frog calls to test for the role of learning. Neurophysiology studies to examine how these different signals stimulate auditory neurons and parts of the brain would also make an important contribution. While passive listening for frog calls presents a number of interesting questions on sensory and perceptual processing, it is just one of the sensory systems used by bats to locate prey. The use of other sensory modalities in foraging decisions is discussed next.

### 11.2.2 Active Listening

The dominant sensory modality of *T. cirrhosus* when hunting frogs clearly seems to be passive listening. *T. cirrhosus* can successfully capture prey with access only to prey-produced sounds such as frog calls. However, these bats echolocate throughout the hunting approach, and studies now show that active listening using echolocation facilitates both prey localization and prey discrimination (Page et al. 2012; Halfwerk et al. 2014a). *T. cirrhosus* echolocates with short (less than 1 ms), multi-harmonic, downward frequency sweeps, which range from 100 kHz to 50 kHz, with most of the call energy at 75 kHz (Barclay et al. 1981; Surlykke et al. 2013). These echolocation calls are very similar to those of other gleaning bat species in the neotropical family of leaf-nosed bats, Phyllostomidae (Falk et al. 2015). *T. cirrhosus* produces echolocation calls for orientation in space and while approaching prey (Barclay et al. 1981; Surlykke et al. 2013). Recent research has also emphasized their importance for determining prey size and for locating prey (Page et al. 2012; Halfwerk et al. 2014a). Experimental evidence even suggests *T. cirrhosus* can use echolocation cues alone to find prey in simple, uncluttered environments (Page et al. in preparation).

A túngara frog call has several by-products stemming from the production of the acoustic signal that offer additional sensory information not only to conspecifics but also to predatory bats. Like many other frog species, the túngara frog has a conspicuous vocal sac that allows it to recycle air, shuttling it back and forth between the vocal sac and the lungs. This dynamically inflating and deflating sac results in a multimodal display by the male frog (Taylor et al. 2008; Taylor and Ryan 2013; Chap. 4). Controlled experiments with a robotic frog (Fig. 11.4) have revealed that both female frogs and bats attend to the dynamically inflating vocal

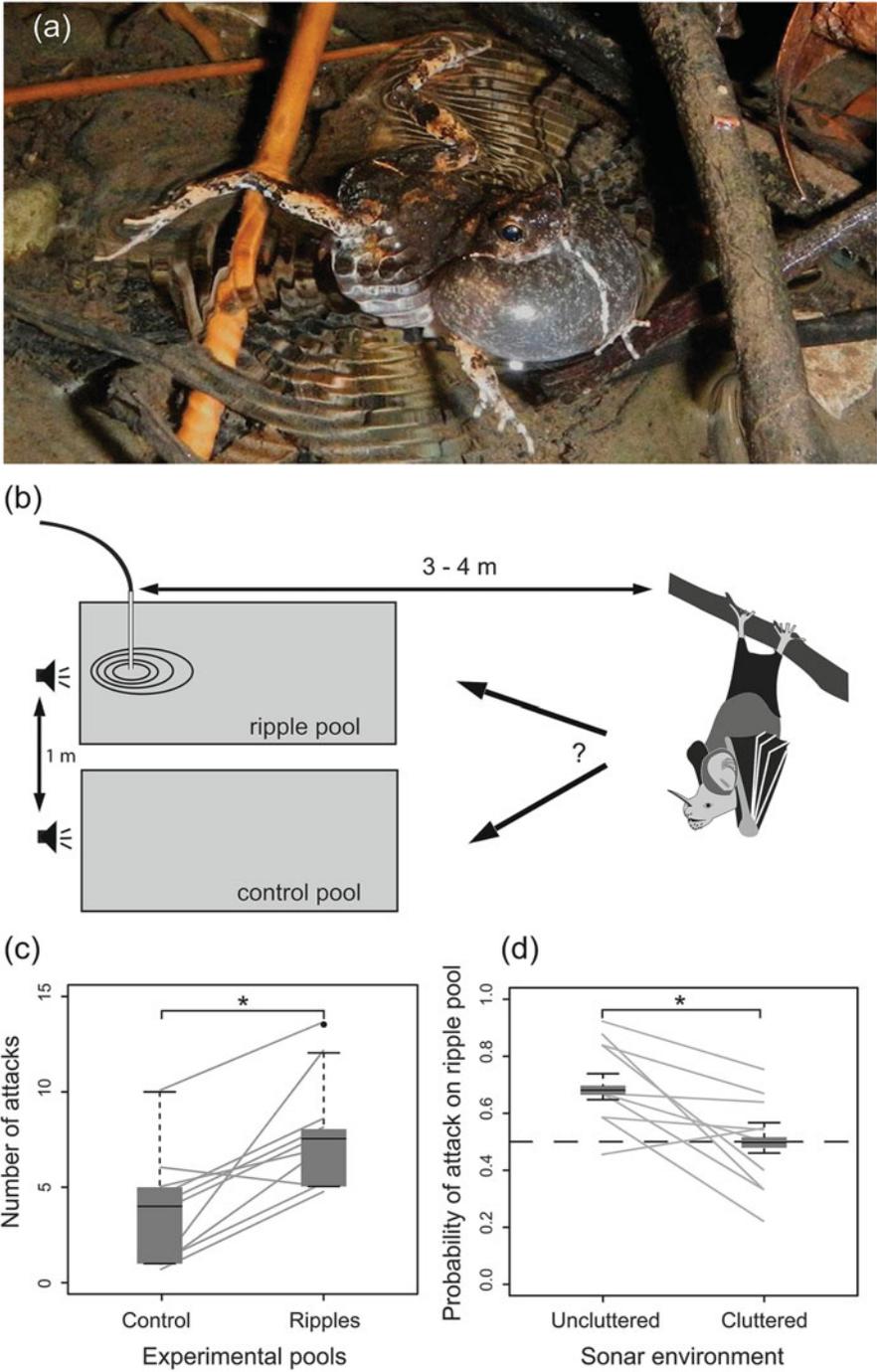


**Fig. 11.4** Real and robotic versions of the túngara frog (*Physalaemus pustulosus*). Photographs in the *upper row* are of an actual calling male shown in different views and states of calling. Photographs in the *bottom row* are of a robotic túngara frog. The robotic frog has a dynamically inflating vocal sac that can be synchronized with its call (see Chap. 4). Modified from Taylor et al. (2008) and used with permission

sac. Coupling motion from this sac with the acoustic signal (the frog call) increases the attractiveness of the call to both receivers, but via different sensory modalities. Female túngara frogs perceive the vocal sac using vision (Taylor et al. 2008). Bat responses to the acoustic signal, however, do not change when offered visual cues, but increase when echolocation is available (Halfwerk et al. 2014a), indicating that bats' perception of the vocal sac is with echolocation, not vision. This is particularly interesting because selective pressures from predators and mates on the same trait are thus mediated by different sensory modalities. Changes to the visual environment will affect sensory access to the multimodal display for females but not for bats, while changes to the echoacoustic environment will affect sensory access for bats but not for female frogs. Thus, environmental fluctuations could create different selective pressures on the mating signal given the differences in sensory access to the signal by mates and predators.

One of the factors that change the environment for a foraging bat is not only the density of frog choruses but also the diversity of calling frogs, as many tropical choruses contain multiple species calling at once. This complexity of sound could make the use of sensory modalities other than passive listening greatly advantageous. The use of multimodal cues is often assumed to improve signal detection and localization amidst background noise. For example, there are a number of frog species in which males call from fast-flowing streams and have evolved additional visual displays such as foot flagging ("semaphoring"), potentially because it makes their signals more salient in a noisy acoustic environment (Hödl and Amézquita 2001). If a multimodal cue makes a signal more salient for a female receiver, it may also make the signal more detectable to an eavesdropping predator. This has been demonstrated for *T. cirrhosus*: bats show more accurate angles of attack when a multimodal cue (robotic frog with inflating vocal sac) is available (Rhebergen et al. 2015). When faced with locating prey amidst heterospecific chorus noise, bats show more directional attacks on the inflating vocal sac model when there are increasing numbers of speakers broadcasting the calls of the heterospecific hourglass treefrog, *Dendropsophus ebraccatus*, which is frequently found calling in mixed species choruses with túngara frogs (Rhebergen et al. 2015). In preference tests, *T. cirrhosus* strongly prefers multimodal prey cues to unimodal ones in background noise, and both reduces the latencies of its attacks and increases its echolocation activity in response to multimodal cues in the presence of background noise (Gomes et al. 2016). The multimodality of the túngara frog call, therefore, does appear to improve localization, directionality, and attack latency for an eavesdropping predator when confronted with increased acoustic background complexity.

In addition to the dynamically inflating vocal sac, there is another signal by-product that males cannot avoid when producing their acoustic signal. Male túngara frogs call while floating on the surface of small pools of water. As they call the movement of their bodies generates water ripples that propagate through the pool (Fig. 11.5a). Frog-eating bats are more likely to attack model frogs with water ripples emanating from their calling location than model frogs with no associated ripples (Fig. 11.5b–d). This is only the case, however, when the pool is clear of leaf



**Fig. 11.5** Fringe-lipped bat (*Trachops cirrhosus*) uses echolocation to detect an unavoidable by-product of signaling by male túngara frogs (*Physalaemus pustulosus*). (a) A calling male

litter and therefore bats have echoacoustic access to the water ripples (Halfwerk et al. 2014b). The detectability of ripples may be an explanation for why túngara frogs are so often found calling from hidden locations underneath leaves and branches. What is so intriguing about the use of water ripples to locate calling frogs is that the ripples propagate into the environment, leaving a trace of where the frog was even if it has stopped calling. Male frogs use the water ripples in order to judge the distance that they are from another calling male in the same pond. Males generally increase their call rate when they are exposed to the call of another male paired with water ripples (Halfwerk et al. 2014b). This unintended by-product of a multimodal signal, therefore, has costs and benefits for the signaling frog and produces another cue that bats can use when locating a target to attack.

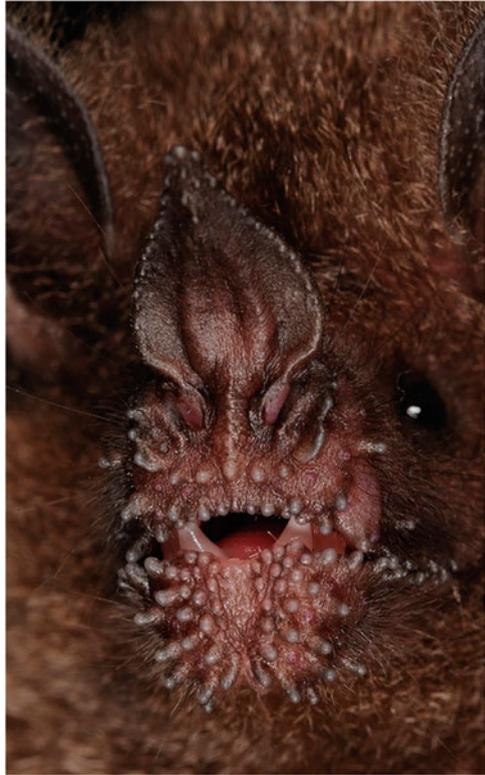
### 11.2.3 Chemoreception

We have discussed the importance of passive listening for prey-generated cues and echolocation to bat foraging decisions. Research has demonstrated that vision does not appear to be an important component of these foraging decisions, at least in approaches to túngara frogs (Halfwerk et al. 2014a). No research to our knowledge has investigated the role of olfaction in prey detection or discrimination with *T. cirrhosus*, although it is known to be very important for other phyllostomid bats, particularly fruit-eating species (Korine and Kalko 2005). Gustatory cues, in contrast, have been shown to be important to prey assessment in *T. cirrhosus* (Page et al. 2012). The role of taste in *T. cirrhosus* is perhaps not surprising given that many anuran species are poisonous. The cane toad, *Rhinella marina*, for example, has toxic parotoid secretions and, if consumed, is lethal to animals much larger than *T. cirrhosus* (Chen and Kovarikova 1967; Bagrov et al. 1993). Possibly to cope with anuran toxins, *T. cirrhosus* appears to have very unusual salivary glands. A study of the submandibular salivary glands of 38 genera of bats revealed that only three bat species, *T. cirrhosus*, *Megaderma lyra* (the greater false vampire bat), and *Megaderma spasma* (the lesser false vampire bat), have submandibular salivary glands containing large, follicle-like structures (Phillips et al. 1987). Later, a fourth species, *Cardioderma cor* (the heart-nosed bat), was found to possess these unusual salivary glands as well (Tandler et al. 1996). All four of these species (*T. cirrhosus*,

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**Fig. 11.5** (continued) túngara frog generates prominent ripples on the water surface while calling. **(b–d)** Bats preferentially approach the call of a túngara frog broadcast near a pool with ripples over an identical call broadcast near a pool of still water. **(b)** Schematic diagram of the experimental setup. **(c)** Results from a two-alternative choice test showing the number of attacks directed toward the ripple pool over the control pool. **(d)** Probability of attack on the ripple pool depends on environmental conditions. When both pools were covered with a layer of leaves (cluttered environment), the bats' preference for ripples disappeared. Graphs in **c** and **d** depict box plots of model estimates and individual lines. Photo in **a** courtesy of Adam Dunn; figures in **b–d** modified from Halfwerk et al. (2014b) and used with permission

**Fig. 11.6** The chin and lips of fringe-lipped bats (*Trachops cirrhosus*) are covered in distinctive tubercles, giving the species its common name. Experiments demonstrate that *T. cirrhosus* can use chemical cues to assess the palatability of its prey (Page et al. 2012). While the tubercles are hypothesized to play a role in this chemo-assessment, enabling the bat to rapidly determine the toxicity of a frog or toad just by brushing its skin, there is no evidence to support this hypothesis to date. The role of these tubercles remains a mystery and is the subject of ongoing research. Photo courtesy Marco Tschapka



*C. cor*, *M. lyra*, and *M. spasma*, respectively, from Latin America, East Africa, and two from Southeast Asia) feed on frogs. It has been hypothesized that the independent evolution of these unique salivary glands could be an adaptation for frog consumption. The saliva may neutralize toxins in the skin of frogs and toads, perhaps allowing bats to prey on less palatable anuran species (Phillips et al. 1987; Tandler et al. 1996).

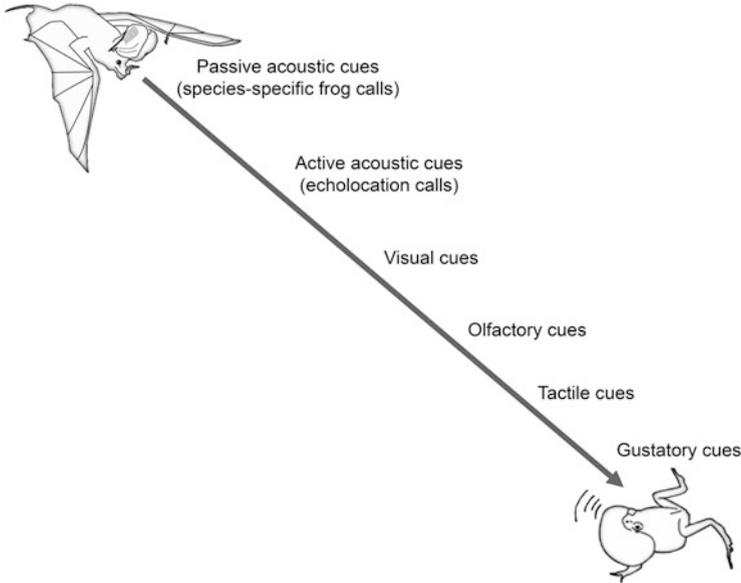
One of the mysteries about *T. cirrhosus*, likely also related to chemoreception, is the distinctive tubercles on this bat's chin and lips (Fig. 11.6). These tubercles give this bat its common name, the fringe-lipped bat, and set it apart from other species. But to date, the function of these tubercles remains unknown. It has been hypothesized that the tubercles allow bats to rapidly assess the palatability of a frog or toad, just by brushing its tubercles to the skin of the prey prior to capture (Miller 1907). However, detailed observations with high-speed video of interactions with palatable and poisonous prey so far show no evidence of the hypothesized brushing behavior (Page et al. 2012). The role of these tubercles is the subject of ongoing investigation. Whether the mechanism is through the tubercles on the chin of *T. cirrhosus* or (more likely) through taste receptors in the mouth, bats use chemoreception in prey assessment (Page et al. 2012). When edible túngara frogs are coated with secretions from the parotoid glands of toads, bats will attack the frogs

but reject them after contact (Page et al. 2012). This study highlights not only the use of chemoreception by *T. cirrhosus* but also the way that multimodal perception of prey cues can be integrated sequentially to influence foraging decisions.

### 11.2.4 Sequential Assessment of Prey Cues

As we have discussed in this section on perception, while passive listening is likely the dominant method used for prey detection by *T. cirrhosus*, foraging decisions are based on multiple cues that enable bats to correct potential errors and alter hunting decisions during, and even after, attack. Cues from different sensory modalities travel at different speeds and across different distances. For bats hunting frogs, the cue that travels the farthest is the male frog's advertisement call. This call likely serves as an acoustic beacon to the eavesdropping bat; it captures the bat's attention and is used by the bat to home in on its prey. As the bat approaches its target, it can recruit additional senses for prey assessment. Echolocation, for example, may be used to detect size, vocal sac movement, or environmental perturbations. When the bat approaches closer yet, olfactory cues may become available, and when it establishes physical contact with the prey, it has the possibility to use tactile and gustatory cues for the final assessment. Thus, different sensory cues are associated with the different stages of the hunting approach, and each offers an opportunity to correct mistakes in prey assessment made using another sensory modality (Fig. 11.7). It is possible that this sequential assessment of prey using multiple sensory cues is what allows frog-eating bats to be as flexible as they are in their foraging decisions, even when foraging amidst highly toxic and size-inappropriate prey.

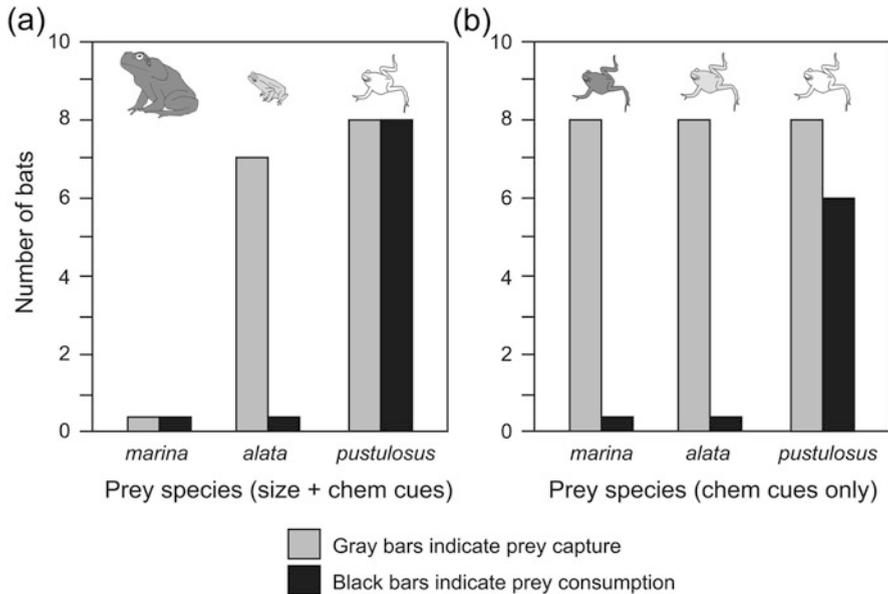
Experimental evidence supports the idea that bats indeed use multiple sensory cues to sequentially refine their prey decisions. When offered conflicting sensory cues—a speaker broadcasting the calls of a palatable túngara frog, topped with a poisonous toad roughly the same size as a túngara frog (the leaf litter toad, *Rhinella alata*) or one much larger (the cane toad, *R. marina*)—bats will approach but veer away from the large cane toad, rejecting it before contact, but will attack the small leaf litter toad, rejecting it only after contact (Fig. 11.8a; Page et al. 2012), suggesting size-based discrimination from a distance, likely by echolocation (Halfwerk et al. 2014a). Likewise, the chemical compounds in cane toad parotoid secretions are not volatile and are secreted only upon contact (Toledo and Jared 1995), so it is unlikely that olfactory cues from these toxins alerted the bats to this toad's distastefulness before contact. It is possible that the bats smell other compounds on the frogs upon close approach. The most likely explanation for the pre-capture rejection of the large cane toad, however, is the bat's use of echolocation as it approaches the prey target. *T. cirrhosus* emits echolocation calls throughout the hunting approach (Barclay et al. 1981; Surlykke et al. 2013). It is very likely that bats approaching a prey item that is far too large for it to handle (and one that may pose a threat and could even consume the bat if offered the opportunity) use



**Fig. 11.7** Hypothesized sequential sensory cue use by the fringe-lipped bat (*Trachops cirrhosus*) during a hunting approach. The frog advertisement call serves as an acoustic beacon to the bat, traveling further than the other sensory cues. As the bat approaches, it can recruit other sensory cues to reassess its decision to attack the prey. Drawings courtesy Kristina Schlegel

information from their sonar signals to reject prey prior to contact (Fig. 11.8a). When bats were offered prey that differed only in chemical cues but not in size (túngara frogs rubbed either with parotoid secretions from the two toad species or with a túngara frog as a control), no frogs were rejected prior to contact. All frogs were captured, but those coated in toad secretions were rejected after the bat had come into physical contact with the prey (Fig. 11.8b). Together, these results suggest a strong reliance on sequential assessment of different prey cues. If assessment mistakes are made at one sensory level, there is the possibility for correction at another, which is perhaps key in enabling this bat to respond to prey cues as flexibly as it does.

Research with humans has shown how information from different sensory systems is weighted through experiments that present subjects with conflicting sensory information (Ernst and Bühlhoff 2004). Further research on how different sensory components are weighted in foraging decisions using behavioral experiments will be important for understanding multimodal decision-making. Future research on *T. cirrhosus* will also hopefully investigate the neurobiology of sensory integration. This complexity in perception of prey cues has made research on *T. cirrhosus* groundbreaking in its insights into decision-making in a non-model system. At the same time, the extraordinary, and charismatic, learning abilities of this predator have captured the attention of cognitive ecologists. In the next section,



**Fig. 11.8** Multimodal assessment of prey by the fringe-lipped bat (*Trachops cirrhosus*). (a) When both size and chemical cues are available, bats reject large poisonous toads (*Rhinella marina*) before capture, but capture and then reject small poisonous toads (*R. alata*). Palatable túngara frogs (*Physalaemus pustulosus*) are consistently captured and consumed. (b) When prey varies in toxicity but not in size, bats make all prey-rejection decisions post-capture. Túngara frogs rubbed in *R. marina* and *R. alata* toxins are captured and released; túngara frogs rubbed with other túngara frogs are captured and consumed ( $N = 8$ ). Modified from Page et al. (2012) and used with permission

we discuss how learning and memory also influence foraging choices, likely overlaid on the complex integration of sensory perception.

### 11.3 Cognition

While research on the role of learning in foraging decisions has historically been conducted with birds, there is a developing literature on the role of learning and memory in bat foraging and social behavior. Variation in learning abilities has been demonstrated across different bat species (Clarín et al. 2013), and there is evidence for learning of group-distinctive vocalizations (Boughman 1997) and social learning of food scents (Ratcliffe and ter Hofstede 2005; O'Mara et al. 2014; Ramakers et al. 2016). *T. cirrhosus*, however, in its learning of species-specific prey cues such as frog calls (Page and Ryan 2005), remains a rare example of the study of cognition in wild-caught bats.

### 11.3.1 *Individual Learning*

Given the perils associated with prey toxicity, one might predict *T. cirrhosus* to exhibit extreme caution when making foraging decisions, with little exploration of novel prey and limited flexibility with known prey. However, there is strong evidence that even though *T. cirrhosus* forages among prey that are both highly poisonous and large enough to consume them (Ibáñez et al. 1999), these bats are extremely flexible in their hunting behavior (Page and Ryan 2005). They exhibit exploratory behavior in response to new stimuli, will generalize their response from the calls of known species to the calls of species they have never heard before (Ryan and Tuttle 1983), and can rapidly learn novel prey cues by observing conspecifics (Page and Ryan 2006; Jones et al. 2013b). They can also use individual experience to reverse established foraging patterns given new information on prey quality (Page and Ryan 2005).

There is substantial evidence that *T. cirrhosus* acquires an individual repertoire of signals they recognize as palatable prey over the course of their lifetime. When wild adult bats are brought into captivity and played frog calls from a speaker, they will readily attack the calls of palatable túngara frogs but will ignore poisonous toad calls (Tuttle and Ryan 1981). However, if a túngara frog call is gradually faded into a toad call using sound editing software, such that each sequential rewarded stimulus sounds less like a frog and more like a toad, within a night, bats will attack speakers playing poisonous toad calls to get food rewards (Page and Ryan 2005). This remarkable flexibility works the other way as well; if túngara frog calls are played repeatedly with no food rewards on the speaker, bats will eventually stop responding to túngara frog calls, although extinguishing the response to a previously positively rewarded cue takes longer than learning a new association (Page and Ryan 2005). The bats are so flexible, in fact, that their ability to learn acoustic stimuli is not limited to frog calls. They can also be quickly trained using stimuli as diverse as Bob Marley songs (R. A. Page unpublished data) and cell phone ringtones (Jones et al. 2013b). This ability to learn new associations very quickly may allow *T. cirrhosus* to develop repertoires of prey signals to which they are responsive and to shift those repertoires with changing environmental conditions such as seasonal changes in the prey species available (Jones et al. 2014).

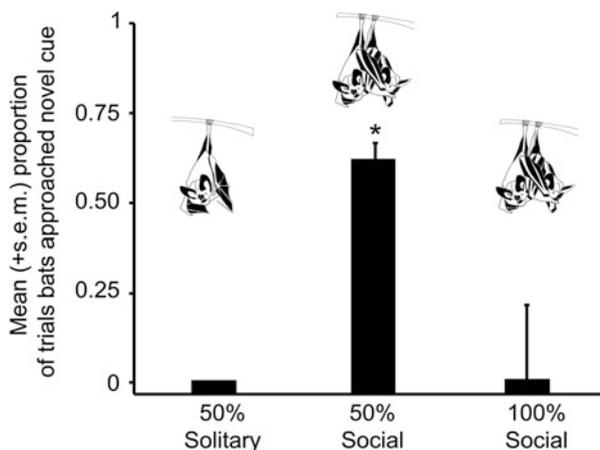
### 11.3.2 *Social Learning*

Foraging decisions can be influenced not only by individual learning but also by acquiring information from conspecifics or social learning. Social learning is widespread in animals, potentially because it allows individuals to acquire information about the environment without incurring the potential risks of trial-and-error learning (Galef and Giraldeau 2001). Social learning of foraging information has been demonstrated for a number of bat species. Among tropical frugivorous bats,

short-tailed fruit bats (*Carollia perspicillata*) learn novel food scents from demonstrators in the roost (Ratcliffe and ter Hofstede 2005), and tent-making bats (*Uroderma bilobatum*) not only learn food scents from conspecifics at the roost but specifically learn them from breath and not from odors on fur (O'Mara et al. 2014). European greater mouse-eared bats (*Myotis myotis*) can learn to associate LED lights with the presence of food and learn this task faster when they can interact with a knowledgeable demonstrator bat (Clarín et al. 2014). Similarly, North American big brown bats (*Eptesicus fuscus*) learn to capture tethered mealworms when allowed to forage alongside demonstrators, with observers and demonstrators flying close together as demonstrators made feeding buzzes in the final stages of attack (Wright et al. 2011). Given the communal roosting and foraging behavior of many bat species, social information may be easily accessible, and for bats that exploit temporary resources, a crucial source of information (Cvikel et al. 2015).

Frog-eating bats roost in small groups in culverts (Handley 1976), caves (Jones 1966), and tree cavities (Kalko et al. 1999; Jones et al. *in review*). Not only do they roost together, studies mounting proximity sensors to these bats have shown that they also associate at foraging sites, such as small ponds (Ripperger et al. 2016). Given the extraordinary diversity of potential prey and their seasonal variation in prey calling behavior, social learning from roost mates could be an advantageous way for frog-eating bats to acquire information about the environment. Social learning of associations between novel prey cues and food quality has been demonstrated in *T. cirrhosus*. If a naïve wild-caught bat is put in a flight cage with a bat that was previously trained to approach toad calls, the naïve bat will approach the toad call in an average of five playback trials (Page and Ryan 2006). If, in contrast, a bat is alone in the flight cage with toad calls playing and food rewards on the speaker, the naïve bats predominantly do not approach the toad calls in 100 trials. Similarly, if two naïve bats are in a flight cage together with these same acoustic stimuli and food rewards, they do not learn the toad calls any faster than a naïve bat alone, eliminating social facilitation as a potential explanation (Page and Ryan 2006). This study shows that *T. cirrhosus* is a fast social learner, providing evidence for another potential mechanism for reducing the costs of approaching novel prey.

Social learning, however, can have drawbacks in terms of misinformation, incomplete information, outdated information, or other costs associated with interacting with conspecifics, such as increased competition (Giraldeau et al. 2002; Laland 2004). The costs and benefits of social information have led researchers to predict that animals should use social information selectively, favoring high-quality (but expensive) individually acquired information under many circumstances (Laland 2004). One of the predicted social learning strategies is that animals should “copy when dissatisfied” (Laland 2004). This has been demonstrated in Norway rats (*Rattus norvegicus*) in which individuals that are fed low-quality diets are more likely to use social information to learn novel food cues than individuals fed high-quality diets (Galef et al. 2008). Similarly, bumblebees (*Bombus terrestris*) foraging on flowers with low sucrose concentration



**Fig. 11.9** The fringe-lipped bat (*Trachops cirrhosus*) uses social information to learn about signals produced by potential food items when their own information is unreliable. Approaches bats made to a novel ringtone depended on the reward schedule of the ringtone to which they had been trained (50 % or 100 %) and on whether or not they had social information about the novel ringtone (Social or Solitary). Bats whose own ringtone was rewarded 50 % of the time and that had social information about the novel ringtone made more approaches than bats that did not have access to social information or bats that had reliable individual information. Modified from Jones et al. (2013b) and used with permission; bat drawings courtesy Damond Kylo

rewards are more likely to use social information to learn alternative flower colors than bees foraging on colors associated with high-concentration sucrose rewards (Jones et al. 2015). This fairly simple social learning strategy is likely widespread in animals and could be a tool many animals use when deciding whether to use social information.

To test whether frog-eating bats are using the social learning strategy of “copy when dissatisfied,” individual bats were trained to respond to one of two cell phone ringtones by fading a túngara frog call into the ringtone as with the toad experiments (Page and Ryan 2006). Bats were then divided into three treatments that differed both in the reward schedule of the ringtone to which the bat was individually trained and in the presence of a tutor bat approaching the alternative ringtone (Fig. 11.9). Bats that only received food rewards on 50 % of the presentations of their trained ringtone were more likely to approach the alternative ringtone, but only when there was a tutor bat demonstrating it (50 % Social). When there was no tutor, bats did not learn the alternative ringtone on their own, but rather continued to forage on their 50 % rewarded ringtone (50 % Solitary). When bats received food rewards for approaching the stimulus they had been trained to 100 % of the time, however, they ignored the social information about the alternative resource (100 % Social, Fig. 11.9, Jones et al. 2013b). Frog-eating bats therefore use social information to learn novel prey stimuli, but do so only under certain circumstances,

weighing the costs and benefits of the sources of information in their foraging decisions.

It is unknown how important social learning may be in the wild. *T. cirrhosus* roosts together, and it is not uncommon to catch two or more adult *T. cirrhosus* in the same net at the same time when using a túngara frog chorus playback as bait (P. L. Jones and R. A. Page unpublished data). This would suggest that multiple adult *T. cirrhosus* could be foraging together and therefore have exposure to social information. Proximity sensors mounted on free-flying *T. cirrhosus* show that roost mates, and in particular what seem to be mothers and their pups, associate at foraging sites in the wild (Ripperger et al. 2016). It is possible that the close association during lactation, potentially extending several months post-weaning, may be a critical time period in which there is extensive social learning of prey cues between mothers and their young.

### 11.3.3 Memory

Not only do frog-eating bats quickly learn novel acoustic stimuli, but they also remember these stimuli for a long time. This may aid bats in hunting ephemeral resources that are only available for parts of the year (Jones et al. 2014). Long-term memory for learned associations between artificial cues and food has been demonstrated for greater mouse-eared bats, in which one individual after a year in the wild remembered the association between an LED light and available food (Clarín et al. 2014). Individuals of *T. cirrhosus* that were trained to fly to cell phone ringtones in the social learning experiment described above were then released back into the wild. Bats captured up to 4 years later still attacked speakers broadcasting cell phone ringtones when brought back into captivity, whereas bats that had not previously been trained to ringtones did not (Dixon et al. in preparation). This experiment demonstrates the extremely long retention of associations between prey and prey-related cues in the wild, which may be necessary for bats that forage relying on ephemeral species-specific prey signals.

## 11.4 Summary and Future Directions

Given its histological and neuroanatomical adaptations, including unique salivary glands and unusually low-frequency hearing suggesting specialization on frogs as prey, it is perhaps surprising to find that *T. cirrhosus* has a wide diet breadth, hunting many taxa in addition to frogs (Bonato et al. 2004), and is not stereotyped, but rather highly flexible, in its foraging behavior (Page and Ryan 2005). The studies reviewed in this chapter examined in detail the interaction between this predator's cognitive flexibility and its sensory and perceptual abilities and how they shape the foraging decisions it makes. Examination of the preference of

*T. cirrhosus* for complex túngara frog calls has led to discoveries about the evolution of sexual advertisement signals from the eavesdropper perspective, in terms of predator localization accuracy, population variation in predator response, auditory processing of different call components, and the role of learning in the preference for signal variants. The túngara frog is only one of a myriad of potential prey species in the Neotropics. The studies described here detail how this eavesdropper is able to be very flexible in its responses to prey calls by updating acoustic information with echoacoustic and gustatory cues as it approaches potential prey, enabling bats to avoid potentially lethal mistakes. Locating a single prey item amidst the cacophony of a frog chorus remains a challenge, however. The use of multimodal components of the frog call, particularly the inflation and deflation of the frog vocal sac and the water ripples generated during calling, enables bats to make more accurate attacks. Finally, the extraordinary flexibility, social learning, and long-term memory abilities of this bat species make it an exciting system in which to study the benefits of cognition to foraging performance.

We see two areas in need of future research. First there is a great need for understanding how animals integrate information from different sensory systems at the behavioral and neural levels. This should be addressed with behavioral experiments to disentangle when bats rely more or less heavily on different sensory systems. These experiments should especially look for cases in which the behavioral responses seem maladaptive, as these can be particularly informative about biases in sensory, perceptual, and cognitive processes. In combination, there is a great need for the integration of neurophysiology with behavioral experiments in order to understand how patterns of neural firing produce the observed behaviors.

The second area in need of research is understanding what the bats are doing in the wild. Studying the behavior of flying animals in dark, dense rainforest is impossible without the use of technological tools. Recent developments in GPS tracking, remote sensing, automated PIT tag readers, and thermal and infrared video are creating new opportunities for studying the behavior of bats in the wild. Knowledge of decision-making in this bat species would greatly benefit from more detailed data on habitat use, roosting behavior, social interactions, and long-term monitoring of individuals. Examining constraints on sensation, perception, and cognition in the wild is crucial to understanding how bats make foraging decisions in the structurally and acoustically complex environment of the biodiverse neotropical rainforest.

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