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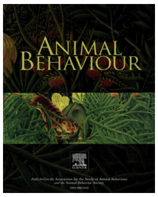

Special Issue: Cognitive Ecology

# ‘Crazy love’: nonlinearity and irrationality in mate choice

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Choosing a mate is one of the most important decisions an animal can make. The fitness consequences of mate choice have been analysed extensively, and its mechanistic bases have provided insights into how animals make such decisions. Less attention has been given to higher-level cognitive processes. The assumption that animals choose mates predictably and rationally is an important assumption in both ultimate and proximate analyses of mate choice. It is becoming clear, however, that irrational decisions and unpredictable nonlinearities often characterize mate choice. Here we review studies in which cognitive analyses seem to play an important role in the following contexts: auditory grouping; Weber's law; competitive decoys; multimodal communication; and, perceptual rescue. The sum of these studies suggest that mate choice decisions are more complex than they might seem and suggest some caution in making assumptions about evolutionary processes and simplistic mechanisms of mate choice.

Infatuation and ‘insanity’ have been inextricably linked in human culture for thousands of years. Today these two conditions are a staple in popular culture and music in many societies (Ryan, 2018). The notion of ‘crazy love’ is based on the premise that persons in love often do not make decisions in predictable or rational ways. As cognitive ecology addresses how animals acquire and analyse information to make decisions (Dukas & Ratcliffe, 2009; Real, 1993), the numerous idiosyncrasies of mate choice should be prime targets for this field.

Ryan, Akre, and Kirkpatrick (2009) recently reviewed various aspects of the role of perception and cognition in mate choice. They focused on issues regarding the acquisition of information by signallers and receivers, and the importance of detection, perception and enhancing signal contrast. At higher levels of cognitive analysis they reviewed studies of categorical perception, transitivity and the seemingly ubiquitous role of early experience influencing later mate choice. There is a wealth of data on how receiver sensory systems acquire and respond to stimuli associated with prospective mates, but far less of an understanding of how higher levels of cognitive analysis influence mating decisions. Ryan and Cummings (2013) updated the literature on perceptual and cognitive biases in mate choice, including the importance of supernormal stimuli and peak shift displacement. Again, that review also revealed the scarcity of studies on cognitive aspects of mate choice.

The state of that field has changed little since then. In a thorough and authoritative review of mate choice, Rosenthal (2017, page 119) indicates that ‘Compared to the vast literature on the sensory basis of mate choice, scant attention has been paid to the evolutionary ecology of higher-order processing in mate choice (but see Ryan et al., 2009; Kelley & Kelley, 2013; Akre & Johnsen, 2014)’. He further states that, although there has been more recent interest in assessment of multimodal or multidimensional mating signals, it is often assumed that the combined effect of these signals on a receiver is simply a sum of its parts. But, as Rosenthal pointed out, there is no reason to think that signal components interact in a simple manner, and he predicted that nonlinearities resulting from interaction of components should be common (also see Stevens, 2014).

Adding to Rosenthal's concern about overly simplistic analyses of multimodal or multidimensional communication is the fact that sexual communication often takes place in complex social environments. The importance of visual scene analysis (Navon, 1977) and auditory scene analysis (Bregman, 1994), involving such phenomena as the cocktail party effect (Bee & Micheyl, 2008; Bee & Miller, 2016), have only recently been addressed in the context of sexual communication and mate choice (e.g. Bee, 2008; Endler &

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Mielke, 2005; Schmidt & Römer, 2011). An important unifying theme in studies of communication in complex visual and auditory scenes is that not all stimuli are what they seem. Illusions abound and cognitive biases often alter the receivers' interpretations of the sexual signals (Stein, 2012).

Understanding how the higher-end of cognitive processes influences mate choice in visual scenes has been most thoroughly explored in bower birds. Endler and his colleagues (Endler et al., 2010, 2014; Kelley & Endler, 2012) have shown that some male bower birds organize bower decorations to elicit a visual illusion known as forced perspective. Although not directly demonstrated, their interpretation is that this forced perspective enhances the visual perception of the males in the eyes of females.

We recently embarked on a research programme aimed at understanding the perceptual and cognitive ecology of acoustic mate choice. We have addressed a number of issues of cognitive biases and mate choice in our study species, the túngara frog, *Physalaemus pustulosus*, taking care to understand not only the underlying mechanisms of these biases but also the evolutionary implications.

## SEXUAL COMMUNICATION IN TÚNGARA FROGS

The túngara frog is a small, 30 mm long, frog widely distributed throughout Middle America and northern South America. As with most frogs, the main component of the mating signal is acoustic (Gerhardt & Huber, 2002), which in this species consists of a whine only (simple call) or a whine followed by one to seven chucks (complex call; Fig. 1). When males call in isolation they tend to produce only whines but add chucks to the whines during vocal interactions with other males (Fig. 1). Females attend to the calls to assess males; a whine is necessary and sufficient to elicit mate attraction, but females have a five-fold preference for complex calls over simple calls (Griddi-Papp, Rand, & Ryan, 2006; Ryan, 1980, 1985).

Males call from a variety of habitats and call predominantly during the rainy season (Fig. 1). Males call in groups, and chorus size can vary from a few to hundreds of frogs. In most cases chorus sizes are about half a dozen. Female frogs are free to exercise mate choice with little or no interference from males. The male's communication channel is not private, however, and is eavesdropped upon by the fringe-lipped bat, *Trachops cirrhosus* (Fig. 1). The bats eat the frogs and rely on the male's call to locate their meal. As with the female frogs, the bats are attracted to whines only but prefer whines with chucks (Ryan, 1985). The same is true for eavesdropping midges, *Corothrella* spp., which take blood meals from the frogs (Bernal, Rand, & Ryan, 2006). Although the primary sexual display is acoustic, there are also associated visual cues (an inflating vocal sac, perceived by the bats by echolocation, but hereafter referred to as visual for simplicity; Halfwerk et al., 2014a; Rosenthal, Rand, & Ryan, 2004; Taylor, Klein, Stein, & Ryan, 2008) and vibratory/seismic cues (ripples generated on the water surface by the inflating vocal sac; Halfwerk, Jones, Taylor, Ryan, & Page, 2014b) that influence responses of both the frogs and the frog-eating bats. Thus there is potentially a large amount of information to be acquired and analysed in the process of making decisions about mates and meals.

We have some understanding of the neural underpinnings of acoustic mate choice in túngara frogs. As with all frogs, there are two inner ear organs sensitive to air-borne sounds: the amphibian papilla, AP, and the basilar papilla, BP (Gerhardt & Huber, 2002). Electrophysiology studies have revealed that the dominant frequency of the whine matches the peak sensitivity of the AP, while the dominant frequency of the chuck is close to the peak of sensitivity of the BP. Thus the whine is primarily and initially processed by one sensory end organ, the chuck by another, and a complex call by both the AP and BP relatively simultaneously. Thus at the level of the peripheral auditory system it appears to be the simultaneous excitation of both sensory end organs that contribute to the enhanced attractiveness of complex compared to

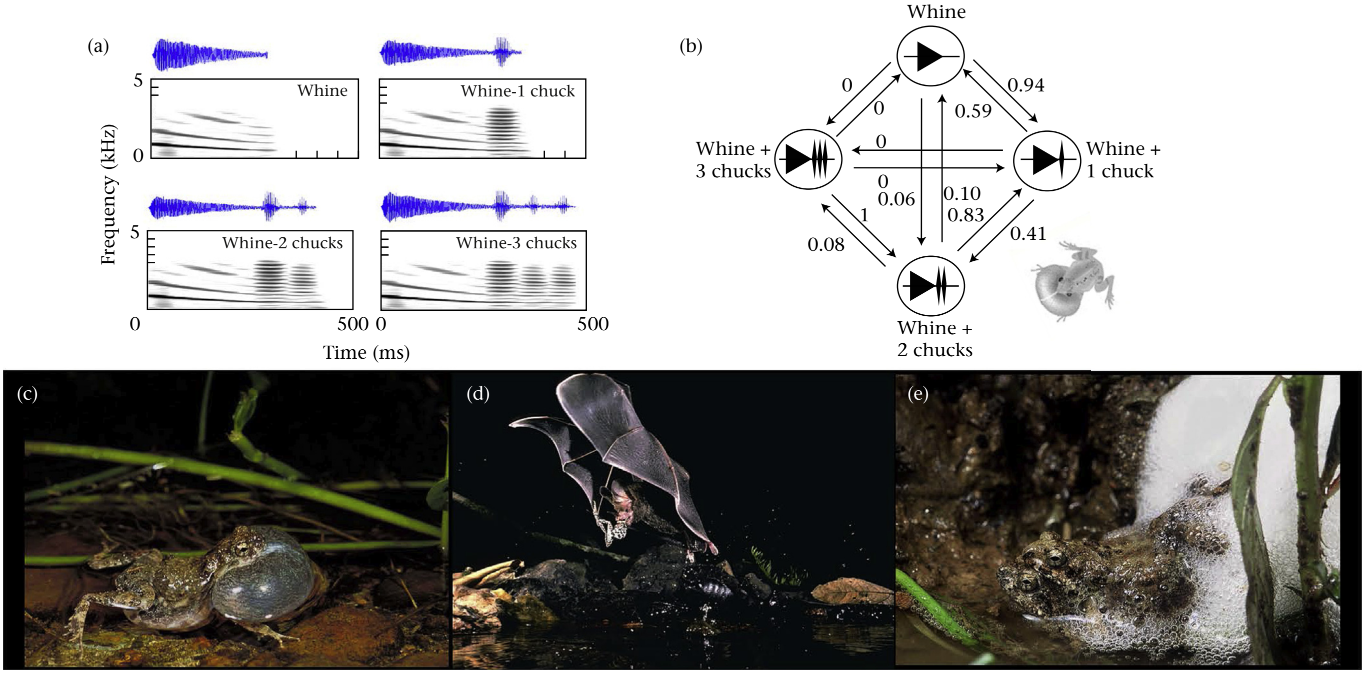

**Figure 1.** (a) Waveforms and spectrograms of mating calls of various complexity: whine, whine-1 chuck; whine-2 chucks; whine-3 chucks. (b) Transition matrix of mating calls of various complexity (from Bernal et al., 2007). (c) A calling male túngara frog (photo by Ryan Taylor). (d) A frog-eating bat, *Trachops cirrhosus* (photo by Merlin Tuttle). (e) A nesting pair of túngara frogs (photo by Ryan Taylor).

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simple calls (Ryan, Fox, Wilczynski, & Rand, 1990; Wilczynski, Rand, & Ryan, 2001).

Processing does not end in the periphery, and we have pursued auditory processing into the central nervous system. In one set of studies, Hoke and colleagues used immediate early gene expression as a marker of neural activity to understand how these incoming neural signals are processed by the brain (Hoke et al., 2004, 2005, 2007a, 2007b, 2010). These studies have shown that differential neural representation of simple and complex conspecific and heterospecific signals involves both changes in mean activity levels across multiple subnuclei in the midbrain, and in the functional correlations among acoustically active areas in the midbrain and the forebrain. In the túngara frog it appears that the auditory midbrain guides behavioural responses to mating calls by acting as a regulatory gateway between the stimulus analysis of the brainstem and the behavioural and physiological control centres of the forebrain (Wilczynski & Ryan, 2010). As detailed as our knowledge is of the neural basis of these preferences, however, it did not predict the cases of nonlinearities and irrationality, outlined below, that seem to characterize mate choice in these frogs. We now review a number of our studies of the cognitive bases of mate choice in túngara frogs which we feel shed light on how complicated a cognitive task this might be.

### *The Chorus is a Cocktail Party: Whose Whine is Whose Chuck?*

How can females exert their preference for calls with chucks in the cacophony of a chorus? The best-known feature of the túngara frog mating system is the five-fold preference for complex calls over simple calls (Griddi-Papp et al., 2006). But to choose a male producing a whine with chucks over a male producing only a whine, the female must be able to assign the correct pair of whine/chuck components to the correct signaller. This is a problem similar to what Cherry (1953) referred to as the cocktail party problem in humans. In a room with a number of people talking, we easily assign an auditory stream, a series of words, to the correct speaker. One can imagine the bizarre conversations we might think we hear if our perceived auditory stream was made up of snippets of speech from different speakers. For many animals the correct assignment of a sound to its source is important in mate choice. We have conducted a number of studies asking to what degree female túngara frogs are able to correctly assign both components of the complex call to the same sound source (see detailed review in Farris & Taylor, 2016).

As noted above, the whine component of the mating call is both necessary and sufficient to elicit phonotaxis from females. The chuck enhances the attractiveness of the whine, but by itself does not elicit attraction from females. Farris, Rand, and Ryan (2002, 2005) used a spatial separation of the whine and the chuck to determine the ability of females to accurately group the two components of the call together. In these studies, females readily approached a speaker producing only a chuck, evidence that there was perceptual grouping of the whine (coming from the other speaker) and the chuck since females will not approach a chuck when no whine is present (Fig. 2). Large grouping angles suggest an inability of the females to accurately group these two call components coming from the same signaller. Surprisingly, females continued to group the two call components together at angles up to 135° (Farris et al., 2002; Fig. 2). These data alone suggest that auditory grouping in the wild must be poor for these females. In a follow-up study, however, Farris and Ryan (2011) showed that when females are presented a whine with two different chucks, all three components being broadcast from spatially separated speakers, the females group the whine and the chuck with the lowest spatial separation. They also showed that when spatial separation is held constant, females are more likely to group together a whine-chuck that occurs in the typical temporal sequence, the chuck being produced shortly after the cessation of the whine. Thus, although females appear quite permissive if not error-prone in their grouping abilities, the larger data set makes it clear that females are able to make more reasonable judgments about sound sources when they analyse multiple spatial and temporal cues (Farris & Taylor, 2016). Thus, in a simple task (one whine and one chuck), females are prone to error when assigning the components to their source. When they are given more information, however (one whine and two chucks), their ability to perceptually group the components improves. In this case, more information is better.

We need to remember, however, that nature is more complex than the laboratory. For example, males usually alternate their calls with one another, but given that the typical call rate is one call every 2 s and the calls are about 300–400 ms, since more than a few males are in the chorus, overlapping calls become the norm. In addition, females can move among the relatively stationary males. We have yet to analyse the vexing problem of how call overlap and the changing position of the receiver relative to the signaller influence source assignments.

### *Adding Chucks and Determining Attractiveness*

Now that we know that under certain conditions females can correctly assign whines and chucks to the correct source, we can ask about the female's preference for chucks. Not only do female túngara frogs prefer calls with chucks to calls without chucks, they also tend to prefer more chucks to fewer chucks, although this preference is proximity dependent (Akre & Ryan, 2010b). How do they make this comparison?

A hallmark of sexual selection by mate choice is the extreme and elaborate traits that evolved in the service of mate attraction (Darwin, 1871; Rosenthal, 2017). The implication is that choosers prefer sexual traits of greater magnitude, and the evidence bears this out. In many cases choosers prefer traits that are larger, brighter, more complex and more intense (Ryan & Keddy-Hector, 1992). Thus it is of some interest to know how different two traits must be to elicit a preference from a chooser. Studies of psychophysics have addressed a similar problem in the context of just noticeable differences (Stevens, 1975), and one important finding is that humans often compare proportional differences rather than absolute differences. The result is Weber's law: $k = \Delta I/I$, in which $k$ is a constant required for a just noticeable difference, $I$ is the magnitude of one of the stimuli, and $\Delta I$ is the difference between two stimuli. It becomes apparent then that as the magnitude of the stimuli increases the difference between them will have to be greater to result in the constant value of $k$. Cohen (1984) pointed out that if choosers follow Weber's law, this could limit the rate of evolution of more elaborate traits (see also Akre & Johnsen, 2014; Bateson & Healy, 2005).

Akre, Farris, Lea, Page, and Ryan (2011) asked if the preference of female túngara frogs for more chucks was based on absolute or proportional differences. They conducted phonotaxis experiments in which females were given the choice between two calls that were identical in all parameters except number of chucks. They asked if the probability that females would choose the call with more chucks was better predicted by the absolute difference in the number of chucks of the two calls or by the proportion of the number of chucks in the two calls. The absolute differences explained only 16% of the variation in the strength of female preference while the proportional difference explained 84% of the variation (Fig. 3). These females are adhering to Weber's law when it comes to comparing numbers of chucks.

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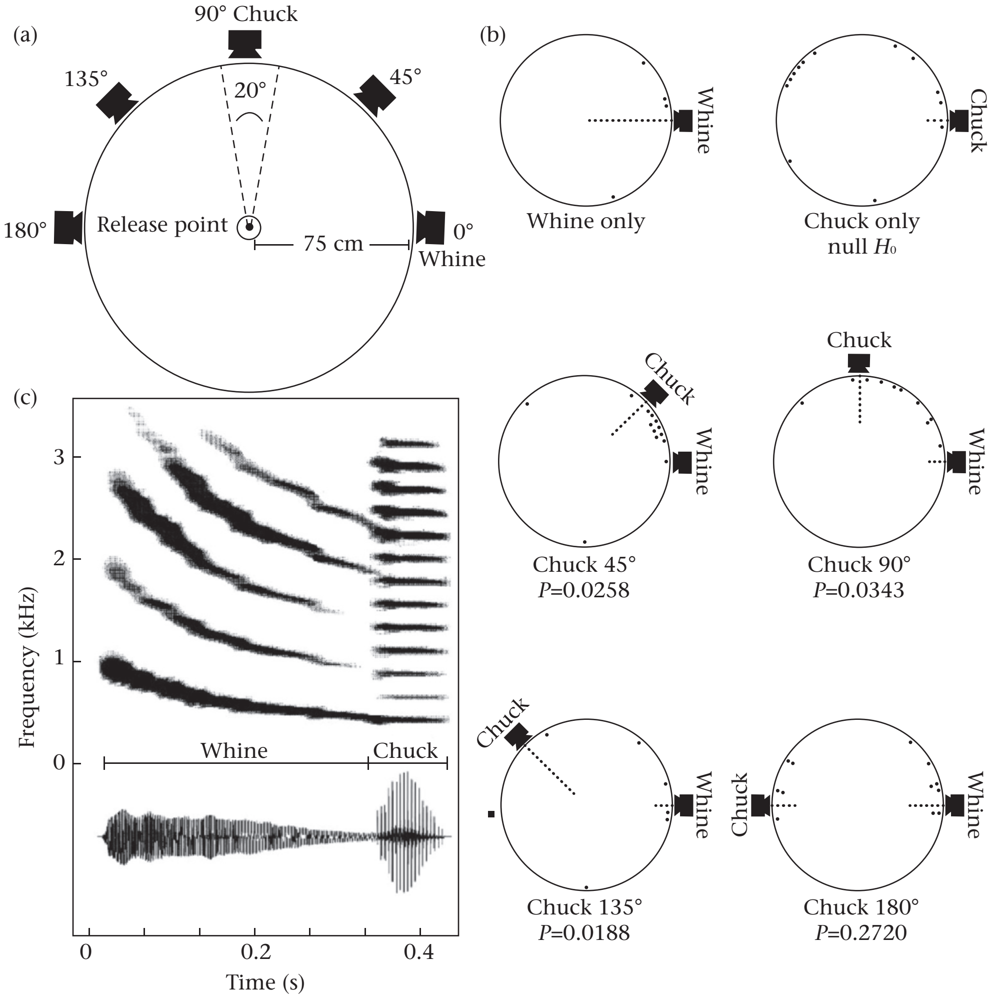

**Figure 2.** (a) Diagram of the phonotaxis arena and an example of one stimulus condition. Five speakers at 45° separation were configured along the perimeter of a 75 cm radius circle on the floor of a sound chamber. Stimuli consisted of a whine and/or a chuck presented together or alone. After release in the centre of the arena, female position and exit angle were recorded using an infrared camera and video recorder. All responses ±10° of the centre of a particular speaker were scored as a positive response to that speaker. (b) Each point represents the exit angle (re: whine position) for one túngara female presented with a whine or a chuck alone or in combination with varying spatial separation. $P$ values are shown for a Fisher's exact test comparing chuck attractiveness when presented with the whine to that when presented alone. Chuck amplitude was 6 dB re: peak whine amplitude (90 dB SPL) (from Farris et al., 2002). (c) Spectrogram and waveform of a túngara frog call.

There are two obvious hypotheses that can explain this pattern of female preference. One is based on the assessment of male quality. If differences in quality map onto number of chucks such that the difference between males producing two versus one chuck is much greater than the difference between males making four versus three chucks, we would expect females to use proportional differences. An alternative hypothesis is that Weber's law reflects a common cognitive algorithm, if so this pattern of female preference might not be an adaptation for mate choice but a more general property of the vertebrate brain. Akre and her colleagues were able to test some predictions of the male quality hypothesis and none of them were supported; for example, call complexity is not correlated with frog length, mass or body condition (Bernal, Page, Rand, & Ryan, 2007). They suggested that a strong test of the cognitive constraints hypothesis would be to ask if a very different animal operating in a different behavioural domain also follows Weber's law when comparing chuck numbers. The frog-eating bat was the ideal candidate for this comparison. Like female túngara frogs it prefers complex calls to simple calls.

They repeated the same phonotaxis experiments with the frog-eating bat with similar results (Fig. 3; Akre et al., 2011). The absolute difference in the number of chucks only explained 8% of the variation while the chuck ratio explained 74% of the variation in the strength of preference (Fig. 3). It appears that Weber's law is not an adaptation for mate choice in túngara frogs but a more general algorithm for comparing stimulus magnitude similar to that found in other animals including humans.

### *How to Remember Who Said What*

Choruses and cocktail parties are not only characterized by spatial variation but by temporal variation as well. Both can fall silent for periods of time before calling and conversation resumes. One challenge for us is to remember what someone was saying before the cloak of silence descended, and a similar challenge is for the female frogs to remember which males were calling, and with what calls, before the chorus attenuated. We know that some signals have evolved to be more memorable, and this is perhaps best understood in the context of warning coloration (Ruxton, Sherratt, & Speed, 2004; Speed, 2000). As summarized by Guilford and Dawkins (1993), naïve birds are more likely to remember which prey is distasteful when the prey is coloured to contrast with its background. Might the chuck do the same for the male túngara frog's call?

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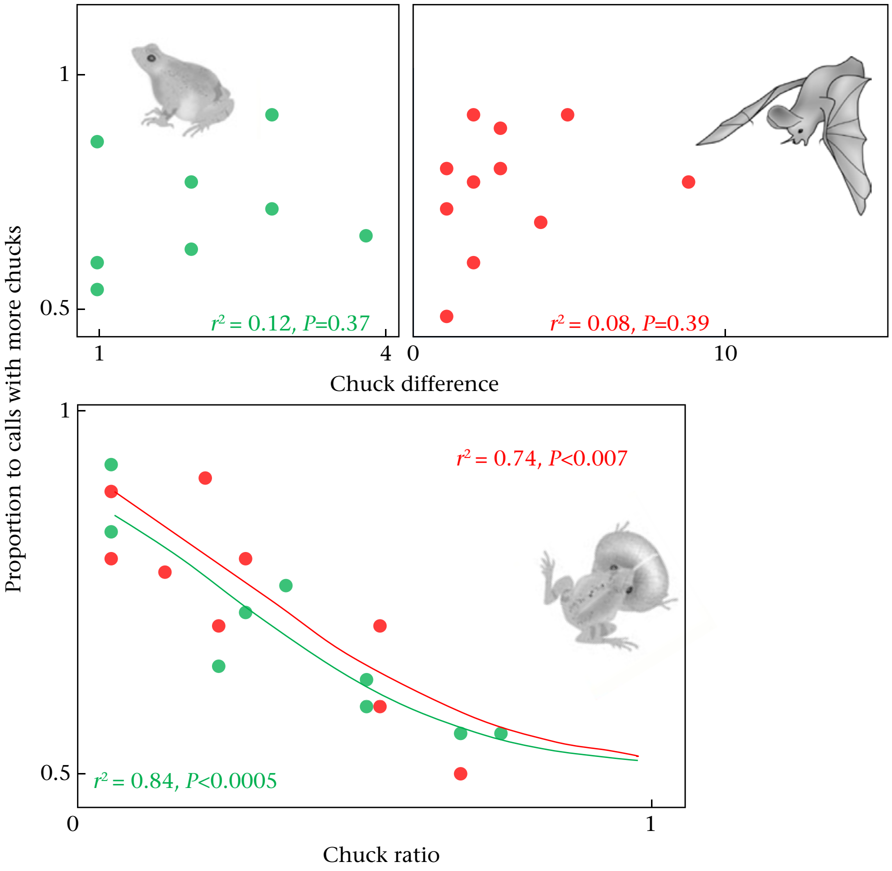

**Figure 3.** Preference response in frogs and bats. Proportions of frogs (🟢) and bats (🔴) choosing the more complex call are shown as a function of (top) chuck number difference and (bottom) chuck number ratio. Curves are the least-squares fit of the psychometric function for data bound by 0.5 and 1 (after Akre et al., 2011).

To answer this question, Akre and Ryan (2010a) recorded 109 chorus bouts of túngara frogs and showed that the bouts are separated by silent intervals that averaged 25.2 s (SE = 1.9). They then conducted phonotaxis experiments in which a female was under an acoustically transparent funnel in the centre of the sound chamber. The female was able to listen to two speakers, for the first 60 s both speakers broadcast simple whines, for the next 30 s one speaker continued to broadcast a simple whine while the other speaker broadcast a whine with either one or three chucks. The presentation was then followed by a silent period of variable time, which was then followed by both speakers again broadcasting simple whines. At that point the funnel was raised and the female was able to approach the speakers. If the female remembered which speaker had broadcast the chuck, then she should prefer that speaker even though the speaker was currently producing a whine. If there was no memory for where the chuck occurred, she should exhibit no preference between the two speakers. There was no evidence of memory for the location of the one-chuck call, but there was for the whine plus three chucks (Fig. 4). The females' memory persisted for some time between 45 and 120 s. As the average silent period between chorus bouts was 25 s, it appears that calls with three chucks could be remembered over that duration.

### *Social Context and Irrational Choice*

Mate choice decisions rarely take place in social isolation. Dugatkin (1992), for example, showed that when a female guppy observed a previously rejected male being courted by another female, that male's attractiveness increased in her eyes. Mate choice copying has been shown in a variety of taxa including other fishes (Schlupp, Marler, & Ryan, 1994) and humans (Waynforth, 2007). Another interesting social context that influences mate choice in humans and other animals is the 'closing time effect'. This phenomenon was first investigated by Pennebaker et al. (1979), who asked rhetorically 'don't the girls get prettier at closing time?' They showed that assessment of other-gender attractiveness by bar patrons increased as closing time of the bar approached. Similarly, Lynch, Rand, Ryan, and Wilczynski (2005) showed that the permissiveness of female túngara frogs towards an atypical synthetic mating call increased towards the end of the night when females were faced with the decision of accepting a mate or dropping their unfertilized eggs at the breeding site.

Social context can also result in decisions being irrational in an economic sense. Economic theory assumes that individuals' decisions should maximize some utility, usually either economic gain or satisfaction (Tversky & Kahneman, 1985). A rational individual adheres to two simple mathematical axioms when she makes a choice: transitivity (if A>B and B>C, then A>C) and regularity (the relative preference of A:B is unaffected by the presence or absence of C). Humans often deviate from these two axioms in making decisions and, when they do, their decisions are considered irrational from an economic perspective (Ariely, 2008).

Deviation from the assumption of regularity is referred to as the decoy effect. For example, *The Economist* offered different subscriptions at the following prices: online subscription, $59; print subscription, $125; print plus online subscription, $125. Sixteen per cent of subjects preferred the online subscription and 84% preferred

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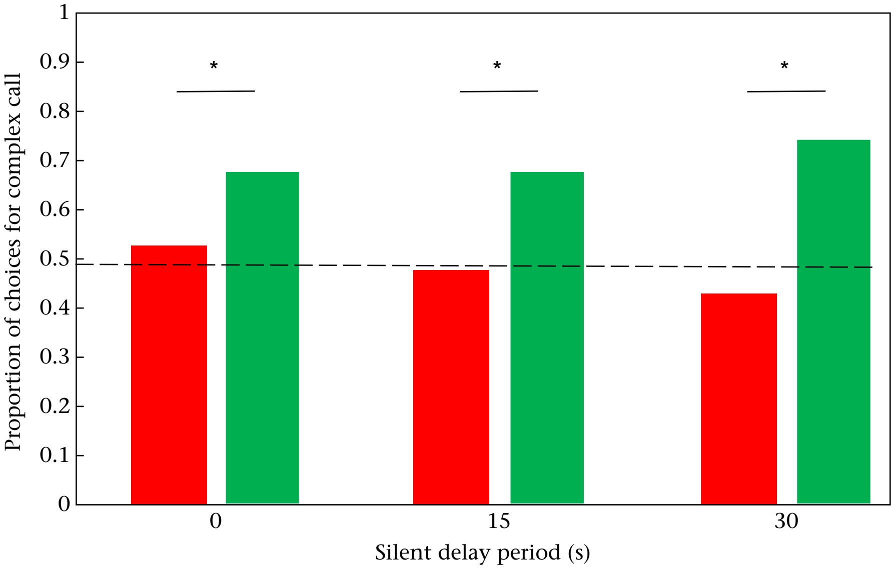

**Figure 4.** Proportion of choices for the speaker that had been broadcasting the complex túngara frog call. Bars show proportion of choices for the speaker that originally broadcast complex calls before a 0 s, 15 s or 30 s silent period. Dashed line shows the null hypothesis of 50% choice for each speaker. Females did not discriminate based on prior calls when the initial call pair was whines versus 1-chuck calls (🟥) but did discriminate when the initial call pair was whines versus 3-chuck calls (🟩), preferentially approaching the speaker that broadcast 3-chuck calls (general estimating equation: $N = 240$ choices, $P < 0.001$; pairwise comparisons with sequential Bonferroni adjustment: $^*P < 0.009$) (from Akre & Ryan, 2010).

the print plus online subscription. Not surprisingly, no one preferred the print-only subscription. Thus, one would imagine that removing that option would have no influence on the relative preference of the online subscription to the print plus online subscription. But that was not the case, the relative preferences changed from 16:84% when all three options were available to 68:32% when only the two options were available. Thus the decision of these subjects was irrational because it was influenced by a competitive decoy (Ariely, 2008). Hummingbirds are also susceptible to competitive decoys when foraging (Bateson, Healy, & Hurly, 2002).

Lea and Ryan (2015) asked if mate choice decisions in túngara frogs were also susceptible to competitive decoys. This is an especially relevant question for animals that choose mates in choruses or leks where there are often more than two individuals being assessed simultaneously.

They presented female túngara frogs with calls that varied on two axes of attractiveness: the acoustic quality of the call and the rate at which it was produced. Females were initially tested with the two most attractive calls in a binary choice situation. There was not a significant preference between calls A and B, although more females preferred call B to call A (Fig. 5). In a trinary test, however, a strong and significant preference for call A emerged even though call C was considered an inferior option (Fig. 5). These results show clearly that there is not an absolute evaluation mechanism used by the females. Not only do these females violate assumptions of economic rationality, they also violate an assumption of most models of sexual selection in that there should be strict preferences, that is 'that all the properties of a stimulus can be reduced to a single preference value that is independent of other stimuli, and that the stronger a female's preference for a male, the more likely she is to choose him' (Kirkpatrick, Rand, & Ryan, 2006, p. 1215).

This is not to say, however, that irrational choice cannot be modelled and predicted. Yukalov and Sornette (2016) applied quantum decision theory to the phenomenon of the decoy effect, in general, and to the results with the túngara frog, specifically. They calculated the quantum probability of how preferences between A and B change from binary to trinary choices. The probability is the sum of a utility factor based on rational evaluation of the subjects and an attraction factor that characterizes irrational, subconscious attitudes of the chooser. Their prediction of how the preferences change between binary and trinary choices shows a remarkable fit to the experimental data in túngara frogs.

### *Multimodal Nonlinearities and Perceptual Rescue*

Communication systems of many animals often seem to operate in a single modality. On closer look or listen, however, it appears that multimodal communication is rampant in the animal kingdom (Hebets & Papaj, 2005; Partan, 2013; Partan & Marler, 1999). A well-known phenomenon in human multimodal communication is the McGurk effect, the phenomenon of hearing lips and seeing voices and the nonlinearities that can result from this interaction (McGurk & MacDonald, 1976).

For most of us, our primary mode of communication is acoustic. Our language is encoded into vocal signals whose primary source of sound is the vocal folds with the trachea, mouth, teeth and lips playing important roles in modifying the sounds that eventually emerge from us as spoken words. Movement of the lips, however, can be apparent to receivers and contains information about their associated words, so much so that our speech can be decoded by lip-reading alone. As most of us have probably experienced, audio–visual integration of the spoken word and associated movements can enhance perception of speech. But interesting nonlinearities that confound our interpretations can emerge when the audio and visual components of speech provide conflicting information. McGurk and MacDonald (1976) presented a video to subjects in which the spoken phoneme was /ba-ba/, but the lip movements were of the phoneme /ga-ga/. Interestingly, neither of those phonemes were perceived by the receiver; instead, subjects heard /da-da/. Do such nonlinearities arise in multimodal communication in other animals? We addressed this issue in túngara frogs.

Frogs do not have lips but they do have vocal sacs (Fig. 1). Analogous to the role of the lips in speech, the vocal sac is an important component of call production in frogs. The vocal sac

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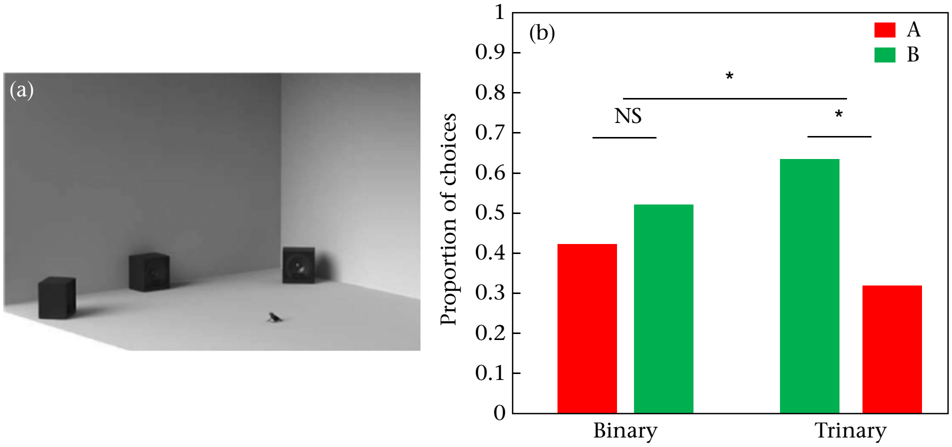

**Figure 5.** (a) The placement of speakers relative to the position of the female for phonotaxis experiments. (b) The proportion of females preferring call A versus call B in the absence (binary experiments) and presence (trinary experiments) of call C ($^*P < 0.05$) (from Lea & Ryan, 2015).

inflates as the call is produced and the air in the vocal sac then returns to the lungs and is recycled within the calling bout of the frog (Bucher, Ryan, & Bartholomew, 1982; Pauly, Bernal, Rand, & Ryan, 2006). But like the lips, the vocal sac can incidentally transmit information during communication, most importantly about the location of the calling male. Although frogs seem to be mostly vocal communicators, the use of visual signals including but not restricted to the vocal sac is widespread throughout the order (reviewed in Hödl & Amézquita, 2001; Starnberger, Preininger, & Hödl, 2014) and túngara frogs are no exception.

Employing video playbacks (Rosenthal et al., 2004) and robotic frogs (Taylor et al., 2008), the investigators showed that the presence of the vocal sac inflating and deflating in synchrony with the call enhanced the call's attractiveness. Following McGurk and MacDonald (1976), they manipulated the relationships between the audio and visual components of the túngara frog's sexual display. They already knew that the temporal relationship of the whine and the chuck was critical for signal salience. For example, female túngara frogs are relatively permissive to changes in the timing of the whine and chuck. Manipulating the placement of the chuck before, during and after the whine still enhances the attractiveness of the whine. There were, however, limits to this permissiveness. Chucks placed 300 ms and 400 ms after the end of the whine resulted in a call that was perceived as a whine-only and not a whine-chuck (Wilczyniski, Rand, & Ryan, 1999). Thus the whine and the chuck must occur in some temporal proximity to be perceptually bound into the percept of a complex call— we also discussed this above in the context of the interaction of spatial and temporal proximity in auditory grouping. The temporal relationship between the acoustic and visual components of the mating call, however, are more stringent. Vocal sac inflation initiated more than 200 ms after the beginning of the call had no effect on the call's attractiveness, and vocal sac inflation immediately following the end of the call actually made the call less attractive (Taylor, Klein, Stein, & Ryan, 2011).

Taylor and Ryan (2013) showed a surprising nonlinearity in the interaction of the call and the vocal sac inflation they termed ‘perceptual rescue’. They showed once again that a chuck temporally displaced from the whine, in this case 500 ms from the end of the whine, resulted in a signal perceived as a simple whine (Fig. 6). They also showed, once again, that vocal sac inflation immediately following the end of the call reduced the attractiveness of the call. They then combined these two stimuli: a whine followed by vocal sac inflation followed by a chuck. This stimulus, whine–vocal sac–chuck was significantly preferred to a whine–silent

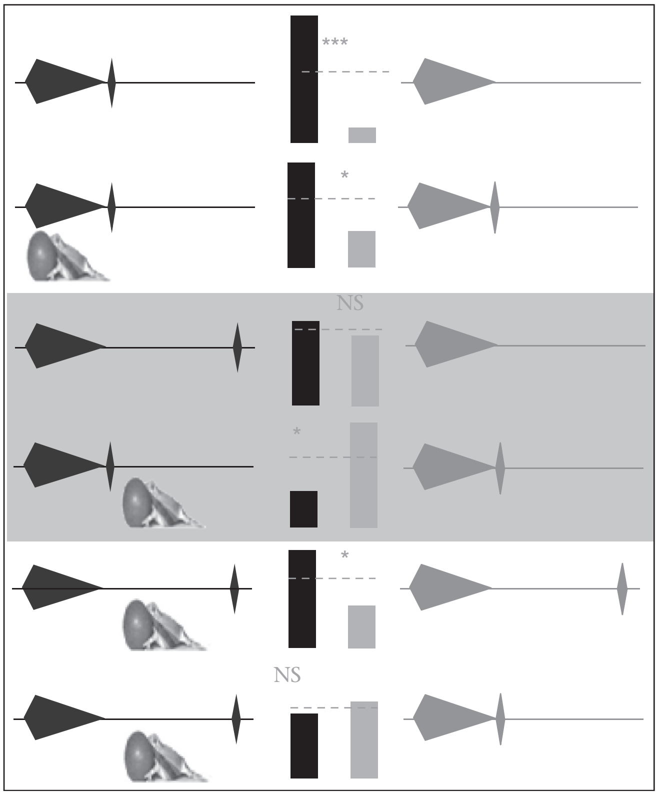

**Figure 6.** Results of phonotaxis experiments between the stimulus on the left (black) and the stimulus on the right (grey). Black bars represent the proportion of responses to the black stimulus, grey bars represent the proportion of responses to the grey stimulus. The image of the robofrog indicates the presence and temporal occurrence of the visual stimulus, an inflating–deflating vocal sac. In the top panel: females prefer a whine-chuck to a whine, and they prefer a whine-chuck associated with an inflating vocal sac versus a whine-chuck with no visual stimulus. In the middle panel: females did not discriminate between a whine with a silent gap followed by a chuck versus a whine only, and females preferred a whine-chuck to a whine-chuck associated with the visual stimulus when vocal sac inflation occurred at the end rather than at the beginning of the call. In the bottom panel: females preferred a whine followed by an inflating vocal sac followed by a chuck compared to the same call without the visual stimulus; the whine–vocal sac inflation–chuck was as attractive as a normal whine-chuck (from Taylor & Ryan, 2013). $^*P < 0.05$; $^{**}P < 0.01$; $^{***}P < 0.001$.

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gap–chuck. In addition, the whine–vocal sac–chuck was as attractive as a typical whine-chuck (Fig. 6). The interpretation is that the displaced vocal sac inflation 'perceptually rescued' the chuck. They hypothesized that this occurs because the displaced vocal sac inflation results in perceptual continuity between the whine and the chuck similar to the phenomenon of auditory continuity that Bregman (1994) and others have shown in humans. Interestingly, pure auditory continuity was not verified when tested in túngara frogs (Baugh, Ryan, Bernal, Rand, & Bee, 2016; Taylor, Page, Klein, Ryan, & Hunter, 2017).

These studies have clearly documented that within the túngara frog communication system, the whine, chuck and vocal sac interact to influence female mate choice decisions (Taylor & Ryan, 2013; Taylor et al., 2008, 2011). The interaction between these signal components is not a simple linear relationship, and signal perception is more complex than a simple template match (either the signal matches a prewired template or it does not). Taylor et al. (2017) further teased apart this relationship by using asynchronous multimodal signals that cannot occur in nature. Generally, if the vocal sac inflation follows the call, females reject the signal. However, they documented that when the vocal sac inflation follows a complex call (whine + chuck), this otherwise aversive call is preferred over a whine that lacks the chuck. When they tested an asynchronous multimodal signal where the visual component preceded the complex call (versus a complex call alone), the females responded to the asynchronous call as often as the unimodal complex call. This suggests that the leading visual signal is less aversive than the lagging signal. Thus, both content and order of signal components play a critical role in audiovisual integration. These asynchrony studies reveal that complex signals are more than the sum of their parts. Furthermore, the multisensory perceptual space of receivers may be much larger than previously thought, providing some of the variance acted upon during signal evolution.

The evolutionary implications of these experiments are of some interest. Perceptual rescue rejects the idea that mate preferences, and more generally receiver recognition, always result from matching incoming signals to a strict neural template (Marler, 1997). We already know that is not true as numerous studies of sensory exploitation and sensory drive have shown (Ryan & Cummings, 2013). These results show just how permissive the female's perceptual landscape can be to evolutionary exploitation by novel stimuli, perhaps fuelling the evolution of elaborate sexual traits that distinguish so many species of animals.

These studies of perceptual rescue were designed to probe the female's preference landscape to determine whether there are hidden preferences for novel trait combinations. One subsequent field observation, however, has shown that these trait combinations might not be totally novel. Ryan, Leslie, and Ryan (2015) reported an unusual observation of a single calling túngara frog in the Darién Forest, Panama. When first observed, this male was producing a call that consisted of only a chuck. Upon further observation the male also produced calls that consisted only of a whine and calls with a whine plus one chuck. Eventually, this male inflated and deflated the vocal sac without making any calls! We certainly do not want to overinterpret this single observation, but it does indicate that the standing phenotypic variation, and perhaps even the standing genetic variation, for sexual communication in this frog is greater than previously anticipated.

## *Is More Information Always Better?*

We conclude this review by asking what might appear to be a rhetorical question. Most events in nature create disturbances that can be perceived by animals through multiple sensory modalities (Balkenius & Dacke, 2010; Clark & Dukas, 2003; Hebets & Papaj, 2005; Partan & Marler, 1999). An approaching predator, for example, might generate cues in the visual, olfactory, acoustic and vibratory modalities. Different animal taxa often invest more heavily in one sensory modality than in the others: olfaction in mammals and hearing in frogs, for example. But we know that most animals are able to recruit additional senses to assess the world around them. This ability seems to be adaptive since more information should increase the ability of the individual to detect important events and make informed decisions about them. We refer to this as the enhanced performance hypothesis (Kulahci, Dornhaus, & Papaj, 2008; Rowe & Halpin, 2013; Siddall & Marples, 2008; VanderSal & Hebets, 2007).

This seems to be true for túngara frogs. The visual cue of an inflating and deflating vocal sac benefits males because it makes the sexual display more attractive to females, and it is probably a benefit to females too as it enhances their ability to locate males. Because túngara frog males call on water, the inflating and deflating vocal sac generates surface-water waves that not only are detected by males, but seem to be used by males as part of a ranging mechanism since ripples travel much slower than the sound of the call (Halfwerk, Page, Taylor, Wilson, & Ryan, 2014c). This is analogous to how we estimate the difference of an approaching storm by noting the difference in arrival time of lightning and the thunder that follows.

But more information is not always better if it is shared with eavesdropping predators and parasites. The visual cue of a vibrating vocal sac increases the male's risk of predation from frog-eating bats (Halfwerk et al., 2014a) as do the water ripples that result from the vocal sac's vibration (Halfwerk et al., 2014b). These extra-acoustic cues associated with calling by male túngara frogs offer alternative sensory channels for the bats to use if signals and cues are being masked by noise in another channel (Gomes et al., 2016). This is not a novel idea, of course, that sexual displays have inherent costs as well as benefits (Rosenthal, 2017; Zahavi, 1975).

Even if we ignore the roles of eavesdroppers, however, we cannot assume that more information is always better. More information will enhance performance only if the brain is able to associate the various stimuli it is receiving, correctly assign them to their particular source and make informed decisions based on the totality of information in the stimuli. If there is too much information to analyse, the individual may experience a phenomenon known variously in human psychology as information, cognitive or perceptual overload (Alsius, Navarra, Campbell, & Soto-Faraco, 2005; Jacoby, 1984; Lavie, 2005; Scheibehenne, Greifeneder, & Todd, 2010; Talsma, Senkowski, Soto-Faraco, & Woldorff, 2010). This overload may result in decreased performance or even maladaptive decisions by the receiver (Clark & Dukas, 1994; Hebets & Papaj, 2005; Rubi & Stephens, 2016). In a recent study on humans, for example, test subjects were less able to evaluate beauty when they were engaged in other cognitive tasks (Brielmann & Pelli, 2017). We refer to this as the cognitive overload hypothesis.

We suggest that animal communication systems are ideal for testing the enhanced performance versus cognitive overload hypotheses because signals commonly incorporate multiple cues in different sensory modalities (Hebets & Papaj, 2005; Higham & Hebets, 2013; Partan & Marler, 1999). The existence of an abundance of cues in multiple sensory channels might sometimes be either a blessing or a curse.

As we have now begun to uncover nonlinearities and irrationalities that arise during mate assessment, we wonder if more assessment of more mate cues is always adaptive, or if it sometimes leads to maladaptive choices that might result from cognitive overload.

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## *Conclusion*

Mate choice, by generating sexual selection, is responsible for the evolution of some of the most spectacular and elaborate traits in the animal kingdom. Thus how animals make mate choice decisions is critical to understanding the evolution of this particular brand of biodiversity. Evolutionary studies have assumed that courtship traits could be reduced to a single value that both predicts mate choice and is independent of other stimuli. Mechanistic studies often assume that the female's preference is defined by an internal template that is better matched by some stimuli than others. Many recent studies, however, have shown that these assumptions of both ultimate and proximate studies need not always hold.

Mate choice decisions often become less predictable when they occur in complex sensory and social scenes; when the metrics of comparison, e.g. linear versus proportional, are not known; and when sensory and cognitive biases result in hidden preferences for previously unknown traits. In addition, our assumption that more information should lead to more adaptive mate choice might not even be true in all cases. Fortunately, all of these complicating issues can be addressed experimentally, which promises to provide us with an even greater appreciation for how and why animals choose the mates that they do.

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