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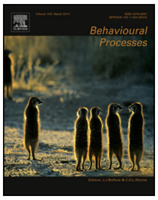

Larger females are choosier in the gray treefrog (*Hyla versicolor*)

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ABSTRACT

Individual variation in female mate choice has important implications for sexual trait evolution and the maintenance of phenotypic diversity. In this study we examined several potential drivers of individual variation in female choosiness for the well-studied, energetically expensive courtship signal of male gray treefrogs, *Hyla versicolor*. Specifically, we investigated the relationship between female choosiness and other female traits (female body size, physical condition, and age) using a costly choice playback experiment where females traveled different simulated distances to reach attractive mates. We found that larger females maintained their preferences for attractive male calls over greater simulated distances (i.e. were choosier) than smaller females. We discuss possible explanations for why larger females may be choosier and suggest several potential avenues of future research.

1. Introduction

Females in many species choose mates based on elaborate sexual displays or ornaments (Andersson, 1994). Historically, these choices have chiefly been studied using pooled observations of many individual females, and were therefore unable to explore whether and how individual females varied in their mate choice behaviors (Jennions and Petrie, 1997; Widemo and Saether, 1999). More recent work suggests that such individual differences in female preference and/or choosiness are potentially common and evolutionarily significant (Jennions and Petrie, 1997; Cotton et al., 2006; Chaine and Lyon, 2008). As a result, the proximate and ultimate causes of individual variation in female choice are now a major area of research among biologists seeking to explain how nonrandom mating and sexual trait variation evolve.

Individual females can differ from one another in several components of the mate selection process that have important evolutionary consequences (for comprehensive reviews see: Jennions and Petrie, 1997; Widemo and Saether, 1999). In order to understand how these aspects of mate choice behavior evolve it is important to consider the many costs and benefits of mate choice (Cotton et al., 2006). In the past there has been extensive research on how trade-offs in males between the benefits of elaborate signals and the costs of producing and maintaining those signals can generate variation in sexual displays and ornaments (Andersson, 1994; Moller and de Lope, 1995; Getty, 2006). Females are likely to face similar trade-offs during mate choice, balancing the benefits and costs of exhibiting mating preferences (Pomiankowski, 1987; Reynolds and Cote, 1995; Cotton et al., 2006). Benefits of mate choice can be direct (access to high quality territories, nuptial gifts, paternal care: Kirkpatrick and Ryan 1991; Forsgren et al., 1996) and indirect (good genes: Petrie 1994; Welch et al., 1998), while costs of choice may include predation and harassment risk, loss of time, energetic costs, missed mating opportunities and risk of disease transmission (Pomiankowski, 1987; Pocklington and Dill, 1995; Backwell and Passmore, 1996; Grafe, 1997; Baugh and Ryan, 2010a). In general females are expected to show weaker preferences and less choosiness when the costs of choice are high (Milinski and Bakker, 1992; Hedrick and Dill, 1993; Slagsvold and Dale, 1994). For example, when forced to swim against a current, female sticklebacks became less selective and were more likely to mate with dull, unattractive males (Milinski and Bakker, 1992).

The kinds of costs and benefits enumerated above are likely to differ among individual females in accordance with multiple extrinsic and intrinsic factors, and thus promote variation in mate choice. These factors include female size (Hingle et al., 2001), condition (Bakker et al., 1999; Hunt et al., 2005; Burley and Foster, 2006; Baugh and Ryan, 2009), age (Kodric-Brown and Nicoletto, 2001; Moore and Moore, 2001), parasite load (Poulin 1994; López, 1999), reproductive state (Lynch et al., 2005, 2006), and prior experience (Dukas 2005; Hebets and Vink, 2007; Bailey and Zuk, 2008).

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For example, in a study of wolf spiders where females and males were raised on either a high or low quality/quantity diet, high-diet females were in better physical condition and were more likely to mate with good condition males raised on high quality diets compared to low-diet females who showed no mate selectivity (Hebets et al., 2008). In house crickets (*Acheta domesticus*), female age was found to influence mate choice with younger females exhibiting a preference for longer male songs with more pulses per chirp, while older females showed no preference (Gray, 1999). In a study of the effects of prior experience, female Polynesian field crickets (*Teleogryllus oceanicus*) raised under silent acoustic conditions were found to be less discriminating among male songs compared to females that were exposed to conspecific song during development (Bailey and Zuk, 2008).

Additionally, certain ecological and environmental factors such as predator abundance (Hedrick and Dill, 1993; Johnson and Basolo, 2003; Bonachea and Ryan, 2011), the physical environment, and timing of the breeding season (Qvarnstrom et al., 2000; Borg et al., 2006; Clark and Backwell, 2015) can influence female mate choice. For example, female green swordtails (*Xiphophorus helleri*) typically prefer to mate with males with long, conspicuous swords; however following exposure to video playbacks of predation events they prefer to associate with cryptic males, presumably to minimize predation risk (Johnson and Basolo, 2003). Female banana fiddler crabs (*Uca mjoebergi*), change their mate selection depending on their location within the inter-tidal zone, and across the breeding season to maximize successful larval emergence (Clark and Backwell, 2015).

We suggest that one of the best ways to understand what drives or limits individual variation in mate choice is to focus on experimentally tractable systems with well characterized mating signals. Here we investigated the influence of body size, condition, and age on female choosiness in the gray treefrog (*Hyla versicolor*). As with many other anuran species, female gray treefrogs assess and select mates based upon specific properties of highly energetically demanding male acoustic advertisement signals (Taigen and Wells, 1985; Gerhardt, 1994). Females prefer long calls, fast call rates, and high call efforts—the product of call length and rate (Gerhardt 1991; Gerhardt et al., 1996; Schwartz et al., 2001), and may receive indirect benefits in the form of improved larval fitness by mating with males producing long calls (Welch et al., 1998). Previous research has documented variation among *H. versicolor* females in the strength of their preference for long calls (Gerhardt et al., 2000), however this is the first study to examine what predicts this variation. In this study we utilized a costly choice playback design where we examined the simulated distances females were willing to travel to reach a more attractive mate to investigate how variation in the intrinsic factors of size, condition and age influence female mate choice. We define females that maintain their preference over greater simulated distances as being choosier. Specifically we tested the prediction that larger and higher condition females would be choosier and willing to travel greater simulated distances to reach a more attractive mate. Larger, higher condition females may be choosier because they are better equipped to handle the costs associated with mate choice than smaller, low condition females. This trend has been observed in empirical studies from multiple taxa (Bakker et al., 1999; Hunt et al., 2005; Hebets et al., 2008), although it should be noted that in a study of túngara frogs, researchers observed the reverse patter with high condition females being less choosy, possibly due to a diminished time for mate choice as high condition females may be closer to dropping eggs (Baugh and Ryan, 2009). Additionally, we predicted that older females would be less choosy because they are closer to the end of their lives when selection for costly mate searching is expected to be weaker (Stearns 1992). In support of this prediction, reduced preference strength and choosiness in older females has been observed in several species (Gray 1999; Kodric-Brown and Nicoletto, 2001; Moore and Moore, 2001).

2. Methods

2.1. Experimental overview

We investigated the influence of female size (length and weight), condition, and age on choosiness using a simulated costly choice playback experiment (e.g. Gerhardt et al., 2000). In this experiment females were presented with a choice between a priori attractive and unattractive male calls that differed in playback amplitude. Because sound pressure level (SPL) is negatively correlated with distance from a sound source (6 dB SPL decrease per doubling of distance), altering playback amplitude simulated males calling from different distances. Numerous acoustically communicating species use signal amplitude as an indication of distance (Naguib and Wiley, 2001). In a previous study of *H. versicolor*, females were observed making smaller movements (shorter walking bouts) when presented with high amplitude calls, which researchers suggested was the result of females interpreting high amplitude as short distance (Beckers and Schul, 2004). We varied SPL between speakers to simulate distance rather than physically separating speakers because it allowed us to simulate a larger range of distances than our lab settings allowed. Additionally, it enabled us to manipulate perceived distance without moving speakers during sets of trials which might otherwise exacerbate effects of individual speakers on stimulus propagation. Although we are confident in our use of variable SPL as a means of simulating distance, we do so with the caveat that in nature females may use other cues in addition to SPL to assess distance (Naguib and Wiley, 2001; Beckers and Schul, 2004; Akre and Ryan, 2010).

While maintaining the unattractive call at a constant "nearby" SPL, we sequentially decreased the SPL of the attractive call simulating a male that was farther and farther away. This method of sequentially decreasing the SPL of the attractive call alternative has been used in previous research to assess female preference strength (Gerhardt et al., 2000). We examined how "far" a female was willing to travel to reach an attractive mate, and whether the simulated distance a female was willing to travel depended upon female size, condition, or age.

2.2. Specimen collection and general testing procedure

Females were collected between May and July 2015 from several breeding aggregations within the Lux Arbor Reserve (Kellogg Biological Station, Michigan State University) in Barry County, Michigan (42°29′N, 85°28′W). Females were collected from amplected pairs to ensure that they were sexually receptive. Mated pairs were brought to the lab and stored in small plastic containers, and kept on ice to delay oviposition until testing (usually within 24 h). All playback trials took place in a simple sound chamber at the Kellogg Biological Station. The chamber consisted of a 2 × 2 m platform covered with a sound dampening blanket and tarp and encircled by draped sound dampening blankets. Speakers (Bose Companion 2 Series II) connected to a HP Envy 15 laptop were placed on opposite ends of the chamber and a small, ~8 cm diameter, hardware cloth cage was placed in the center between the two speakers. All testing took place under dark conditions, and a night-vision capable camera (VideoSecu Bullet Security Camera, Model IR24W) was mounted above the chamber so that female responses could be observed remotely. Before testing, containers with the mated pairs were removed from ice and females were given ~1 h to warm up, which previous studies have shown is sufficient time for female body temperature to reach room temperature (Bush et al.,