



# Context and condition dependent plasticity in sexual signaling in gray treefrogs



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## ABSTRACT

For many species sexual signaling is a very costly activity, both in terms of energetic expenditure and increased conspicuousness to predators. One potential strategy to limit the costs of signaling is to only signal at maximum effort in contexts when signaling is expected to be most effective. Multiple studies have documented extensive plasticity in sexual signaling within a variety of contexts, however fewer experiments have examined individual-level variation in the extent of signaling plasticity and the causes of this variation. In this study we examined the influence of size and physical condition on the magnitude of signaling plasticity using a gray treefrog (*Hyla versicolor*) study system. We quantified signaling plasticity by recording male calling behavior first in the absence and then in the presence of a sexually receptive female. For one call property, call length, we found that both weight and condition had a significant influence on the magnitude of plasticity. Smaller males, and males in higher condition exhibited the greatest degree of plasticity. We discuss several possible explanations for this pattern and provide suggestions for future work to examine the consequences of this plasticity and the potential interactive effects of multiple biotic and abiotic contexts on signaling plasticity.

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## 1. Introduction

Males from a wide variety of taxa produce elaborate displays to attract potential mates (Anderson and Iwasa, 1996). When these signals differ between individuals, females often prefer to mate with males who produce larger, and/or more intense displays, which are often assumed to communicate some aspect(s) of male quality (Grafen, 1990; Getty, 2002; Dall et al., 2005). These preferred (intense) signals can incur multiple costs for male signalers including, for instance, energetic demands and conspicuousness to predators. While these costs can constrain male signals (Anderson, 1994; Magnhagen, 1991; Prestwich, 1994; Zuk and Kolluru, 1998), the costs can sometimes, in principle, be ameliorated by behavioral plasticity. In general, behaviorally plastic male signalers are predicted to reserve intense (and costly) signals for the contexts that maximize anticipated fitness returns (Patricelli et al., 2002). Despite extensive evidence that signal plasticity is common in nature (reviewed below), it is still common practice to ignore individual-level variation in signaling plasticity (but see Peretti

et al., 2006; Bertram et al., 2013; Sullivan-Beckers and Hebets, 2014).

Previous work shows that changes in sexual signaling can be induced by a variety of abiotic and biotic environmental conditions. Males in several species adjust their signaling behavior to overcome abiotic constraints on signal transmission and efficacy (McNett et al., 2010; Wilgers and Hebets, 2011; Montague et al., 2013). For example, male blue-black grassquits (*Volatinia jacarina*) accelerate their display rates in direct sunlight, which maximizes the conspicuousness of their iridescent plumage to female receivers (Sicsu et al., 2013). In the wolf spider (*Schizocosa ocreata*), where males use both visual and seismic signals to attract females, males accentuate visual signal components whenever substrate restricts vibratory signal propagation (Gordon and Uetz, 2011).

There are also many examples of males adjusting signals in response to biotic variation, including the presence of conspecific rivals, the proximity and behavior of receptive females, and presence of potential predators (Kelso and Verrell, 2002; Patricelli et al., 2006; Akre and Ryan, 2011; Gavassa et al., 2013; Kim and Velando, 2014). Male zebra finches (*Taeniopygia guttata*), for example, produce redder bills in the presence of female conspecifics (Gautier et al., 2008). In a study of the Australian toadlet (*Pseudophryne bibronii*), nesting males accelerated their calling rates in the pres-

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ence of receptive females (Byrne, 2008). And in the fiddler crab (*Uca perplexa*), males increase claw waving when females approach (How et al., 2008). In each of these examples, male signaling plasticity appears to minimize signal cost/benefit ratios, and thereby maximize expected payoffs to males. This, in turn, should promote or maintain plasticity in male signaling behavior (Patricelli et al., 2002; Sullivan-Beckers and Hebets, 2014).

Although previous studies have measured individual variation in sexual signaling plasticity, the factors that drive this variation have received considerably less attention. A complete understanding of the drivers behind variation in the magnitude of plasticity is crucial to building a more comprehensive model of behavioral plasticity (Bretman et al., 2011). What research has been done indicates that multiple factors can influence the magnitude of plasticity (Jacot et al., 2008; Bertram et al., 2013; Fitzsimmons and Bertram, 2013). In the special case of alternative mating tactics, previous research has found a variety of intrinsic characteristics such as body size, physical condition, and age can interact to catalyze a plastic switch between reproductive tactics (Howard, 1984; Gross, 1996; Leary et al., 2005; Wilgers et al., 2009; Humfeld, 2013). For example, in Woodhouse's toad (*Bufo woodhousii*) and the Great Plains toad (*Bufo cognatus*) males adopting a "satellite" reproductive strategy, who remain silent and target females lured by their rivals' calls, were found to be significantly smaller than males producing mate attraction calls (Leary et al., 2005). Smaller males may deplete energy reserves required for sustained calling more rapidly than larger males, or smaller males may be less attractive to females making costs of calling outweigh the benefits, leading to the adoption of a "satellite" strategy. Similarly, in green treefrogs (*Hyla cinerea*), males in poor physical condition were more likely to switch mating tactics to a "satellite" strategy than high condition competitors (Humfeld, 2013). These examples underscore how the adoption of different mating tactics may be influenced by individual variation in some aspect of status (size, condition, age, etc.) These same characteristics may influence less extreme forms of behavioral plasticity and may affect the extent to which males modulate their signaling in response to abiotic and biotic environmental variables.

In this study we investigate signal plasticity (1) in response to the presence or absence of females, and (2) as it related to male size (length and weight), and condition (after controlling for correlations with age; see methods section). Our model for this study, the gray treefrog (*Hyla versicolor*), exhibits several features that make it well-suited to studies of inter-individual variation in signaling plasticity. Like many other anurans, gray treefrogs produce acoustic advertisement calls to attract females (Gerhardt, 1994), and these calls are very energetically costly to produce (Taigen and Wells, 1985; Wells and Taigen, 1986). Females base mate choice decisions on certain call properties, preferring long calls, rapid call rates, and high call efforts, a composite of call length and rate (Gerhardt, 1991, 1996; Schwartz et al., 2001). In this study we chose to focus on these temporal call properties because they are highly dynamic (Gerhardt, 1991, 1996), and as such these properties are more likely to exhibit signal plasticity. Previous research has shown that male gray treefrogs alter their calling behavior in response to varying levels of vocal competition, typically producing longer calls at shorter rates as competition increases (Wells and Taigen, 1986; Schwartz et al., 2002). Additionally, males have been shown to increase their calling behavior in the presence of females, producing call lengths and call efforts approaching the upper limit of signal performance for this species (Fellers, 1979; Reichert and Gerhardt, 2012; Reichert, 2013). Although these studies document extensive signaling plasticity, the extent and causes of individual-level variation in signal plasticity remain unexplored.

In this study we test whether male treefrogs that differ in length, weight and/or condition exhibit differences in behavioral response to female presence. Specifically, we predicted that smaller, poor

condition males would show a greater escalation in calling behavior in the presence of females than larger, high condition males. Our rationale was that the extreme energetic demands of calling (Taigen and Wells, 1985; Wells and Taigen, 1986) may be more difficult to bear by smaller, poor condition males, and as a result, these males should restrict high signaling effort to contexts where mating is most likely to occur (such as proximity to receptive females). Additionally (or alternatively), small males may face tradeoffs between energetic investments in signaling and growth that are less limiting for larger males (Stearns, 1992; Hoglund and Sheldon, 1998; Heino and Kaitala, 1999).

In contrast to small males, large and high condition males may exhibit less dramatic responses to female proximity because (a) they can readily maintain high signal effort, at comparatively low cost, even when mating is unlikely, and/or (b) females can identify and prefer these larger and/or higher condition males (Gatz, 1981; Morris, 1989), obviating any need to increase calling effort above a baseline level.

## 2. Methods

### 2.1. Specimen collection and testing apparatus

Male and female gray treefrogs were collected between May and July 2013 from the Lux Arbor Reserve (Kellogg Biological Station, Michigan State University) in Barry County, Michigan (42°29'N, 85°28'W). Individuals were collected from several ponds within the reserve as amplexed pairs (to ensure that females were sexually receptive), and brought back to the lab for testing. All recordings took place under dark lighting conditions within a simple sound chamber at the Kellogg Biological Station consisting of a 2 × 2 m platform covered with a sound-dampening blanket and tarp, and encircled by additional draped sound-dampening blankets.

### 2.2. Recording signal plasticity

To examine the signaling plasticity of males in response to female proximity we recorded male calling behavior in the absence and presence of a nearby female. At the start of testing, isolated males were placed in a small (~10 × 10 cm) wire cage in the center of the sound chamber. We recorded 20 consecutive calls produced in the absence of a female as a baseline of comparison. Recording began after approximately 1 min of calling to allow males to establish consistent calling behavior and minimize any warming up period. Following baseline recordings, we placed a single receptive female in a separate wire cage adjacent to the male and recorded an additional 20 consecutive calls. We followed other investigators in their decisions to perform all tests in the same order (recordings of baseline calling behavior followed by recordings in the presence of stimuli, e.g., Wells and Taigen, 1986; Reichert and Gerhardt, 2012; Reichert, 2013). This approach is commonly used because male responses to manipulated stimuli can persist for unknown periods of time following stimulus removal, and thus complicate interpretation of results (Reichert and Gerhardt 2012). To confirm that the changes in male calling we observed were caused by the addition of female stimuli, we analyzed a random sample of 10 recordings of males calling in the field (recorded for a separate study in 2011) over comparable time spans as the trials in this study (~2–3 min). This showed no systemic changes in calling behavior over the course of the recording and a paired t-test revealed no significant difference in call length from calls sampled at the beginning of the recording versus calls sampled near the end ( $t = -0.86$ ,  $df = 9$ ,  $p = 0.41$ ). All recordings were made using a Sennheiser ME 66 microphone and K6 power supply connected to a Marantz PMD620 digital recorder. Male snout-vent-length (SVL) was measured to

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