

May 2014

# The Effect of Female Quality on Mating Preferences in the Eastern Gray Treefrog

Robb C. Kolodziej

*University of Wisconsin-Milwaukee*

Follow this and additional works at: <https://dc.uwm.edu/etd>

 Part of the [Biology Commons](#)

---

## Recommended Citation

Kolodziej, Robb C., "The Effect of Female Quality on Mating Preferences in the Eastern Gray Treefrog" (2014). *Theses and Dissertations*. 712.

<https://dc.uwm.edu/etd/712>

This Thesis is brought to you for free and open access by UWM Digital Commons. It has been accepted for inclusion in Theses and Dissertations by an authorized administrator of UWM Digital Commons. For more information, please contact [open-access@uwm.edu](mailto:open-access@uwm.edu).

THE EFFECT OF FEMALE QUALITY ON MATING PREFERENCES IN THE  
EASTERN GRAY TREEFROG

by

Robb C. Kolodziej

A Thesis Submitted in  
Partial Fulfillment of the  
Requirements for the Degree of  
Master of Science  
in Biological Sciences

at

University of Wisconsin-Milwaukee

May 2014

## **ABSTRACT**

### **THE EFFECT OF FEMALE QUALITY ON MATING PREFERENCES IN THE EASTERN GRAY TREEFROG**

By

Robb C. Kolodziej

The University of Wisconsin-Milwaukee, 2014  
Under the Supervision of Dr. Gerlinde Höbel

Understanding the mechanisms driving female mate choice is critical to developing a holistic framework from which to assess effects and outcomes of sexual selection. I investigated the effects of female quality (measured as size, body condition and fecundity) on preferences for call traits that indicate either male quality (call duration) or species specificity (call pulse rate). I document large variation in both quality and call trait preferences of individual female Gray treefrogs, and show that preferences are influenced by female quality. Contrary to previous studies, however, I found that intermediate quality females show the strongest preferences, while low and high quality females show similar, and weaker, preferences. Further, preferences for male quality were influenced by more quality measures than preferences for species specificity, suggesting that species recognition is somewhat more immune to quality effects than choice for conspecific mate quality.

## TABLE OF CONTENTS

|  |    |
|--|----|
| List of Figures .....  | iv |
| List of Tables .....   | v  |
| Acknowledgments.....   | vi |
| Introduction.....  | 1  |
| Methods.....   | 4  |
| 1) Study site.....   | 3  |
| 2) Playback and stimulus design.....   | 4  |
| 3) Female quality.....   | 6  |
| 4) Female preferences.....   | 7  |
| 5) Description of female preference function and analysis of quality effects....                       | 7  |
| 6) Statistical analysis.....   | 8  |
| Results.....   | 10 |
| 1) Variation in female quality .....   | 10 |
| 2) Variation in female preferences.....  | 10 |
| 2a) Preference for call duration.....  | 10 |
| 2b) Effect of quality on call duration preferences .....   | 11 |
| 2c) Preference for pulse rate .....  | 12 |
| 2d) Effect of quality on pulse rate preferences .....  | 12 |
| 3) Correlation between call duration and pulse rate preferences .....                                  | 13 |
| 4) Difference between call duration and pulse rate preferences .....                                   | 13 |
| Discussion.....  | 13 |
| 1) Effect of size/age on female preference .....   | 14 |
| 2) Effect of condition on female preference .....  | 15 |
| 3) Effect of fecundity on female preference .....  | 16 |
| 4) Is species recognition or conspecific mate choice more strongly affected by<br>female quality?..... | 17 |
| 5) Implications for sexual selection.....  | 17 |
| Figures.....   | 20 |
| Tables.....  | 29 |
| References.....  | 33 |

## LIST OF FIGURES

Figure 1 - Preference function metrics: Peak; a measure of the call trait with the fastest response, Response effort; a measure of the average response across all call traits measured, Tolerance; a measure of the width of the preference at 70% of the peak response and Preference strength; the squared coefficient of variation in responses across all call traits, for an open functions (top) and closed functions (bottom).  
.....20

Figure 2 - Distribution of female quality measures in terms of a) SVL, b) condition index and c) clutch size (N=82).....21

Figure 3 - Correlation of quality measures a) SVL Vs. Clutch size ( $F_{1, 81} = 52.14$   $P < 0.0001$ ) b) condition Vs. clutch size ( $F_{1, 81} = 2.67$   $P < 0.11$ ) and c) SVL Vs. condition ( $F_{1, 81} = 24.71$   $P < 0.0001$ ). SVL was strongly correlated to both condition index and clutch size.....22

Figure 4 - Distribution of preference function traits for call duration a) peak b) response effort c) tolerance and d) preference strength (N=82). .....23

Figure 5 - Distribution of male calls sampled for a) call duration and b) pulse rate. Female average preference functions by condition (High = black solid line, Medium = blue large dashed line, Low = red small dotted line), grouped by mean +/- 1 standard deviation being medium and above and below respectively the high and low groups. SVL (n= 13 high, 57 medium, 12 low) for c) call duration and d) pulse rate. Clutch size (n= 15 high, 52 medium, 15 low) for e) call duration and f) pulse rate. Body Condition (n= 12 high, 57 medium, 13 low) for g) call duration and h) pulse rate.....24

Figure 6 - Significant interactions between call duration response variables and quality measures. a) Individuals of intermediate SVL had higher response efforts b) individuals of intermediate condition had larger tolerances... .....25

Figure 7 - Distributions of preference function traits for pulse rate a) peak b) response effort c) tolerance and d) preference strength (N=82).... .....26

Figure 8 - Significant interactions of pulse rate response variables with quality measures. a) individuals with intermediate SVL had higher response effort b) individuals with intermediate SVL had weakest preference strengths.....27

Figure 9 - Correlation of female preference traits across call stimuli. Female a) response effort was strongly correlated ( $F_{1, 81} = 566.7$ ,  $P < 0.0001$ ,  $R^2 = .87$ ) as was b) preference strength ( $F_{1, 81} = 23.1$ ,  $P < 0.0001$ ,  $R^2 = .21$ ) however c) tolerance ( $F_{1, 81} = .41$ ,  $P < .5217$ ,  $R^2 = 0.00$ ) was not across duration and pulse rate trials.....28

## LIST OF TABLES

|  |    |
|--|----|
| Table 1 - Analysis of responses of gray treefrog females (N=82), testing for the effect of female quality on responses to variation in call duration. Significant P-values are highlighted in bold.....  | 29 |
| Table 2 - Clutch size did not affect preference traits for call duration, but females of different SVL and condition showed differences in response effort and tolerance (condition only). Female quality never affected peak preference or preference strength. Significant P-values are highlighted in bold..... | 30 |
| Table 3 - Analysis of responses of gray treefrog females (N=82), testing for the effect of female quality on responses to variation in pulse rate. Significant P-values are highlighted in bold.....   | 31 |
| Table 4 – Clutch size did not affect preference traits for pulse rate, but females of different SVL and condition showed differences in response effort and preference strength (SVL only). Female quality never affected peak preference or tolerance. Significant P-values are highlighted in bold.....          | 32 |

## ACKNOWLEDGMENTS

I would like to acknowledge the people that have helped me in my pursuit of a Master of Science degree. First I would like to thank my advisor, Gerlinde Höbel for her patience and tolerance as she guided me throughout the process. Her contributions have been invaluable to the final project, and my development as a scientist. I would also like to thank Erik Wild for encouraging my interest in science and research as an undergraduate as well as participating on my graduate Committee. I would also like to thank committee members Peter Dunn and Andrew Petto, who both contributed significantly to my writing. For maintaining stability in the lab and helping me in the field, I would like to thank my lab mate Diana Kim. For help in the field and lab, I would like to thank Phil Beudry, Megan Helt-Baldwin, Patrick Walsh, Jessie Prepodnik, Ben Brennan, Stephan McGuire, and Wonsoek Jang. I would like to thank James David Pampush for providing some outside perspective throughout the process. Finally I would like to thank my parents Dennis and Sharon Kolodziej and my wife Britta Binek Kolodziej for emotional support and encouragement.

## Introduction

Variation in mate choice behavior is important because of the dramatic evolutionary consequences resulting from sexual selection on male phenotypes (Hunt et al. 2005; Jennions & Petrie 1997). Identifying the origin and maintenance of variation in female preferences is a critical step in understanding the role of sexual selection in the co-evolution of male traits and female preferences for those traits. Despite growing interest in the patterns of variation of female preferences, the causes of variation in preferences remain poorly understood (Anderson 1994; Cotton et al. 2006b; Jennions & Petrie 1997). Frequently, mate preferences are dependent on environmental factors such as predation risk (Magnhagen 1991), parasite load (Lopez 1999), age/experience (Kodric-Brown & Nicoletto 2001), body condition (Hunt et al. 2005), and relative cost of choice imposed by predators in the environment or the cost of maintaining oocytes beyond a certain time (Hedrick & Dill 1993; Moore & Moore 2001).

In particular the relationship between female preferences and female quality has captured attention. Like male traits, female preferences should be costly to maintain (Bookmythe et al. 2008; Jennions & Petrie 1997; Slagsvold & Dale 1991), and higher quality females are expected to better bear the costs associated with mate choice (Alem & Greenfield 2010; Cotton et al. 2006b; Iwasa & Pomiankowski 1991; Kokko et al. 2002). Indeed, several studies found evidence supporting the link between preference and quality (Bos et al. 2009; Hunt et al. 2005; Lerch et al. 2013; Riebel et al. 2009).

Yet, quality is a difficult concept to capture in one or a few measures, and not surprisingly, definitions of quality vary greatly among studies. Quality has been measured by means of body condition indices, body size, age, major histocompatibility



complex, and relative disease load (Hale et al. 2009; Kotiaho 2000; Laucht & Dale 2012). A link between female age and female preference has been demonstrated in multiple taxa (Anjos-Duarte et al. 2011; Coleman et al. 2004; Kodric-Brown & Nicoletto 2001; Moore & Moore 2001). Generally these studies reveal a relatively linear relationship of age with preference, with older females being less selective (Anjos-Duarte et al. 2011; Coleman et al. 2004; Kodric-Brown & Nicoletto 2001; Ligout et al. 2012; Moore & Moore 2001; Wilgers & Hebets 2012). In organisms with short generation time amenable to lab rearing, age can be assessed with relative ease. Field studies aiming to assess individual age are at a disadvantage. However, in many taxa individuals continue to grow after reaching sexual maturity (i.e., many invertebrate as well as lower vertebrate taxa), such that body size correlates with age (Lykens & Forester 1987; Sagor et al. 1998). This allows for the use of body size as a proxy for age, which may then be related to female preferences.

The costs associated with the expression of female preferences should be modulated by the energy reserves that are available for mate choice behavior, as well as by the energy reserves that have been invested in reproduction (Jennions & Petrie 1997). For example, females with larger energy reserves should be better able to cope with the cost of mate choice, predicting that females in better condition are more selective. Studies generally use body condition indices, i.e., size-adjusted measures of relative body mass, to estimate energy reserves, and several studies have found a relatively linear relationship between condition and preferences (Baugh & Ryan 2009; Hebets et al. 2008; Hedrick & Kortet 2012; Holveck & Riebel 2010; Hunt et al. 2005; Lerch et al. 2011; Lerch et al. 2013; Riebel et al. 2009; Woodgate et al. 2010). Further, females with higher investment

in a given mating event should also be choosier because they have more to lose from a bad mate choice decision. Although never investigated in connection with female preferences, fecundity might be a particularly good measure of quality relating to mate preferences, especially in organisms with pulsed reproduction where clutch size provides a direct measure of current reproductive investment (Perrill & Daniel 1983; Ritke et al. 1990; Wells 1976).

Amphibians offer an excellent opportunity to investigate the relationships between female quality and mate preferences, due to their well characterized preferences for call traits, indeterminate growth, easily assessed body condition and external fertilization. I studied the effect of female quality on call preferences in Eastern Gray Treefrogs (*Hyla versicolor*). During the spring and summer breeding season, male *H. versicolor* form choruses at woodland ponds and produce pulsed advertisement calls to attract females. Female *H. versicolor* discriminate among males based on various call parameters, namely call duration and pulse rate (Gerhardt 1991). Females prefer longer calls (Gerhardt 1991), which have been linked to better larval performance (Doty & Welch 2001; Welch 2000; Welch et al. 2002). Females also prefer calls with pulse rates near 20Hz (Gerhardt 1991). The calls of a closely related species (*Hyla chrysoscelis*) are centered at 50Hz (Gerhardt 1994) suggesting that pulse rate is involved in species recognition. Thus, call duration and pulse rate are involved in different contexts of mate choice, and focusing on female preferences for either trait allowed me to assess how quality might affect different aspects of female choice (conspecific mate choice and species recognition, respectively).

I tested two hypotheses about the causes of variation in female mate preferences. The first hypothesis posits that female quality influences female preferences. This hypothesis

makes the prediction that high-quality females (i.e., larger/older females, females in better body condition, and females with larger egg clutches) will show stronger preferences for long calls and calls with a species-specific pulse rate than low quality females. The second hypothesis posits that there will be an interaction between female quality and the context of choice (conspecific mate quality vs. species recognition). Since choosing the wrong species carries more severe penalties than choosing a low quality conspecific, preferences associated with species recognition should be less strongly associated with quality than preferences associated with conspecific mate choice. This hypothesis therefore makes the prediction that there will be a tighter correlation between female quality and preference for longer duration calls than to calls of the correct pulse rate. By using 3 quality measures (size/age, condition, and clutch size) and detailed descriptions of female preferences through the construction and analysis of entire preference functions (Fowler-Finn & Rodriguez 2012; Rodriguez et al. 2006) this study examines the effect of female quality on female choice at an unprecedented level of detail.

## **Methods**

### **Study site**

Amplectant pairs of frogs were collected from the University of Wisconsin-Milwaukee (UWM) Field station in Saukville WI during the 2010 breeding season (April-July).

Females were transported to UWM, and kept in coolers at 2° C. Females were acclimated to room temperature 30 minutes prior to testing. All playback trials were conducted at 20°C to control for effects of temperature on female preference (Gerhardt 1978).

### **Playback setup and stimulus design**

For testing, females were placed in a circular, acoustically transparent (hardware cloth) cage, which was located 1m from the playback speaker within a playback chamber covered in anechoic foam. Females were tested using a no-choice paradigm in which response latency to a given stimuli is used as a proxy for interpreting preferences across the range of tested stimuli (Bailey 2008). After the stimulus was played 3 times, the lid of the release cage was removed remotely. Female movements were observed under infrared illumination via a closed circuit video system. A positive choice was scored if a female moved within 10 cm of the speaker broadcasting the stimuli, at which point the time it took the female to reach the speaker was recorded. If a female did not show phonotactic behavior within 5 minutes the trial was recorded as a “no response”. “No Responses” were excluded from statistical tests, but included (coded as infinitely long approach latencies) for the construction of preference functions. Experimental calls were generated using a custom designed computer program (written by Joshua J. Schwartz) and amplified before being played back from the speaker at an amplitude of 85 dB SPL at the position of the release cage. Testing stimuli for call duration (pulses per call) covered the range from 6 pulses (280 milliseconds) to 42 pulses (2070 milliseconds) per call at intervals of 6 pulses for a total of 7 stimuli. The test series for pulse rate stimuli ranged from 8 to 40 Hz, with smaller intervals located around previously reported peak in preference of 20-25Hz (Gerhardt 1991) for a total of 11 stimuli. Pulse rate stimuli were held constant for duration being 18 pulses in length. Both sequences bracketed the natural variation in male call traits with at least 1 stimulus above and below the natural

range observed in the population (Diana S. Kim unpublished data).

Each female was tested with 21 different test stimuli: 7 testing call duration preferences, 11 testing pulse rate preferences, 1 two-choice experiment testing species identification, and 2 standards (stimuli of average pulse rate and duration as sampled from the population being tested). The first trial for each female was a two-choice trial testing species recognition between *Hyla versicolor* and its sister species *Hyla chrysoscelis*. The study population is within the range for *H. chrysoscelis* and this test was to confirm that all females being tested were *H. versicolor*. The second trial and final trial were always a call of population average pulse rate and duration to test for female fatigue throughout the trial. All other stimuli were tested in random order. A fatigue effect was not evident during preliminary trials using either the standards ( $F_{2,162} = 1.33$ ;  $P=0.27$ ) or the entire playback sequence ( $F_{2,1638} = 0.95$ ;  $P=0.52$ ).

### **Female quality**

I obtained three measures of female quality: (1) body length (SVL), which may be related to age (Lykens & Forester 1987; Sagor et al. 1998), (2) a body condition index, which provides a measure of maintained body mass per body length, and (3) clutch size as a measure of reproductive investment. Clutch size measurements were obtained by placing females with their original amplexant male in a container measuring 30 cm x 16.5 cm x 9.5cm filled with 6.5cm of aged tap water and allowed to oviposit. Clutch size was later tallied using photographs taken with Cannon Powershot S5IS digital camera. Post oviposition, each female's weight (to the nearest 0.1g with a pesola spring scale) and SVL (snout-vent length) (to the nearest 0.1mm with calipers) were recorded. From these

body measures a body condition index was calculated for each female, using the residuals from a linear regression of the cube root of body mass divided by body length on body length (Baugh & Ryan 2009; Howard & Young 1998). Post oviposition weights were used for the regression in an effort to control for variation in individual fecundity investment and water regulation which may confound pre-oviposition mass measures. Upon completion of a test series all females were marked using both toe clips and alpha numeric tags (Northwest Marine Technology, Inc.) and released at the capture site.

### **Description of female preference function and analysis of quality effects**

A female mate preference can be thought of as function valued trait that represents the female's propensity to make mate choice decisions across a given range of male traits (Hunt et al. 2005). Preferences functions can be categorized as either open, in which the preference for the male trait in question has no relative upper limit, or closed, having an optimum male trait value from which anything below or above are discriminated against. Preferences function curves, can be further dissected into the traits that characterize them, such as their responsiveness, tolerance, strength and peak (see Fig 1) (Bailey 2008; Fowler-Finn & Rodriguez 2013; Rodriguez et al. 2013). Preference function shape as well as preference function traits can vary between females, and this variation makes the whole preference function a trait of interest when investigating sexual selection (Rodriguez et al. 2013).

Preference functions were created using cubic splines (Dolph Schluter, <http://www.zoology.ubc.ca/~schluter/software.html>) of inverse transformed response latencies with 10,000 bootstrapped replicates. Cubic splines are smoothed piece-wise

polynomial functions used to fit an approximate curve to data which minimizes the total curvature while bending through multiple data points. The “stiffness” ( $\lambda$ , Lambda) of the function was adjusted on an individual basis based on an analysis of best fit using a cross validation score of best-fit report (GCV score) in the same software.

For visual inspection of preference function shape as a function of female quality, the sample of tested females was divided into three quality groups, using the mean female quality measure  $\pm 1$  SD to determine group ranges. The medium group contained any individual that was within  $\pm 1$  SD from the mean and high and low groups contained females above or below this group, respectively. Average preference functions for each of the 3 quality groups were created using average response latencies within quality groups. These average times were then inverse transformed and preference functions were created using cubic splines as described above.

To further investigate female preferences, individual preference functions were generated for all tested females ( $n=82$ ). From these preference functions I obtained four quantitative preference traits: 1) peak, the trait value eliciting the fastest response; 2) response effort, a females' average response latency across all stimuli for a given male trait (duration and pulse rate, respectively); and two measures of selectivity; 3) tolerance, measured as preference function width at 70% of peak, (for open function the highest value tested acted as the upper boundary to the preference function); and 4) preference strength, a measure of how strongly a female discriminates her favorite from her least favorite trait value, calculated as the squared coefficient of variation ( $CV^2$ ) in response latency (see Figure 1). Each of the four preference traits was then correlated with female quality measures using linear and quadratic regressions.

## **Statistical Analysis**

To test for overall variation in female preferences and their correlation with female quality, response sequences were analyzed using random-regression linear mixed models. Models included female identity as a random factor, linear and quadratic terms for call stimuli (call duration or pulse rate, respectively), linear and quadratic terms of female quality measures (SVL, body condition or clutch size, respectively; log transformed to normalize data), and the interaction between stimulus and female quality terms. Linear terms represent female response as a function of increasing or decreasing call trait (an open preference) while quadratic terms represent female response as a curved function in relation to increasing or decreasing call trait (a closed preference). Significant interaction terms indicate variation in preference function shape relative to a given quality term.

To test whether there was individual variation in preference traits irrespective of call trait under investigation, I calculated correlations between preference traits for call duration and pulse rate. Response effort and preference strength values are directly comparable between traits. To compare tolerances, it was necessary to account for differences in the maximum preference function width arising from differences in the range of tested stimuli. Therefore, tolerance scores were standardized as a percentage of the maximum (i.e., 36 for duration and 32 for pulse rate), with a maximum tolerance equal to 1.0. Preferences for peak were not compared due to inherent differences between traits. Analyses were performed in JMP Version 7.0.



## **Results**

### **1- Variation in female quality**

Female quality showed a broad range of variation. SVL ranged from 38.5 mm to 55.5 mm (Figure 2 a). Maintained body condition ranged from -0.094 to 0.076 (Figure 2 b). Clutch size ranged from 325 to 2062 (Figure 2 c).

SVL showed a strong positive linear correlation to both clutch size (Figure 3a) and maintained body condition (Figure 3b), whereas the relationship between maintained body condition and clutch size was non-significant (Figure 3c).

### **2- Variation in female preferences**

#### **2a- Preference for call duration**

Population-wide, females showed a preference for longer-duration calls, which is indicated by the significant linear stimulus terms in the model (Table 1). This is corroborated by visual inspection of the population preference function (Fig 5c, e, and g) and the histogram of peak preferences of individual females (Fig 4a). 51% of females preferred the stimulus with 42 pulses per call (Figure 4a ), which is 75% longer than the longest call produced by males in the study population (Figure 5a, unpublished data from Diana S. Kim).

There was substantial between-female variation in preferences for call duration. Most females preferred the longest-duration stimulus, but individual female peak preferences covered the entire sequence tested, from 6 to 42 pulses (Figure 4a).

Response efforts ranged from 0.0063 to 0.0788 (Figure 4b). Tolerances ranged from 7 to 36 pulses, with most females showing high tolerance values (Figure 4c). Preference strength ranged from 0.0114 to 0.7472, with most females showing low preference strength (Figure 4d).

## **2b- Effect of female quality on call duration preferences**

Clutch size did not have an effect on female preferences for call duration (Table 1, Table 2 and Figure 5g), but both SVL and condition did (Table 1, Table 2 and Figure 5c and e).

The significant quadratic SVL term in the GLM indicates that female size did affect preferences for call duration (Table 1). The analysis of individual preference function traits showed that this variation was due to differences in response effort (Table 2), with intermediate-size females showing greater effort (faster response latencies) than either small or large females (Figure 6a). Peak preference, tolerance and preference strength, however, were not affected by female SVL (Table 2)

The significant interaction term between stimulus and maintained body condition indicates variation in preference function shape across female body condition (Table 1; see also Fig 5e). The analysis of individual preference function traits showed that this variation was mainly due to differences in selectivity (tolerance) (Table 2), with females of intermediate body condition showing higher tolerances (wider functions) than females in either low or high condition (Figure 6b). Female peak preferences response effort and preference strength were unaffected by body condition (Table 2).

### **2c- Preference for pulse rate**

Significant linear and quadratic terms of stimulus pulse rate indicate that females prefer intermediate value for pulse rate (Table 3). Population-wide, the majority of females preferred the intermediate stimuli values (Figure 7a) which roughly corresponds with the distribution of male calls sampled from the population (Figure 5b, unpublished data from Diana S. Kim).

There was large between female variation in preferences for pulse rate. Peak preferences covered the entire sequence tested, from 8 to 40 pulses per second (Figure 7a). Response efforts ranged from 0.0049 to 0.069 (Figure 7b). Tolerances ranged from 5 to 32 pulses per second (Figure 7c). Preference strengths ranged from 0.0607 to 0.7125 (Figure 7d).

### **2d- Effect of female quality on pulse rate preferences**

Preferences for pulse rate were not affected by clutch size or body condition (Table 3, Table 4), but the significant quadratic SVL term indicates that female preference for pulse rate is affected by size (Table 3; Figure 5d). The analysis of individual preference function traits showed that this variation was due to differences in response effort (Table 4) with intermediate-sized females showing higher response effort than either small or large females (Figure 8a), and to differences in selectivity (preference strength), with females of intermediate size showing lower preference strengths than either small or large females (Figure 8b).

### **3- Correlation between call duration and pulse rate preferences**

Response effort was significantly positively correlated between pulse rate and call duration trials (Figure 9a), as was preference strength (Figure 9b). Tolerance, however, was not correlated between the preferences for different traits (Figure 9c).

### **4- Difference between call duration and pulse rate preferences**

Female preferences for pulse rate stimuli (indicating species specificity) were less correlated with quality measures than preferences for call duration (indicating male quality), but the difference was not very pronounced. SVL was the only quality measure significantly affecting pulse rate preferences (significant effect of SVL x SVL, Table 3), while both SVL and maintained body condition significantly affected call duration preferences (significant effect of SVL x SVL, and significant interaction of Stimulus x Condition, Table 1). The effect of body condition is the biggest difference between the two preferences, solely effecting call duration preference function shape.

## **Discussion**

I tested whether variation in call preferences of female Gray treefrogs related to variation in their quality, measured as among-female variation in size, body condition and fecundity. I did find large variation in both female preferences and female quality, which provides the potential for the evolution of quality-dependent mating preferences. Overall, my data is in line with previous research in so far as I document that preferences are affected by body condition (Bakker et al. 1999; Baugh & Ryan 2009; Cotton et al. 2006a; Engqvist 2009; Hebets et al. 2008; Hunt et al. 2005), body size (Cotton et al. 2006a;

Hedrick & Kortet 2012; Holveck & Riebel 2010; Rintamaki et al. 1995; Slagsvold et al. 1988), and age (Anjos-Duarte et al. 2011; Kodric-Brown & Nicoletto 2001; Ligout et al. 2012; Moore & Moore 2001; Wilgers & Hebets 2012), but not by fecundity (Cotton et al. 2006b). However, while previous studies generally report that females that are larger, younger or in better condition show stronger preferences (but see (Ahuja et al. 2011; Baldauf et al. 2013; Griggio & Hoi 2010; Robinson & Morris 2010; Syriatowicz & Brooks 2004), in my study it was the intermediate size, age or condition class that showed strongest preferences, while the responses of extreme quality individuals (either high or low) were often similar and lower.

### **Effect of size/age on female preferences**

In Gray treefrogs, body size (SVL) had the largest effect on preferences, affecting response effort in both pulse rate and call duration trials, and affecting selectivity (tolerance) for pulse rate. In anurans, age and size are frequently correlated (Halliday & Verrell 1988), suggesting that the link of preference to SVL may actually indicate underlying age-dependent preferences. Age-dependent variation in preferences seems to be common (Anjos-Duarte et al. 2011; Coleman et al. 2004; Jennions & Petrie 1997; Kodric-Brown & Nicoletto 2001), but while I found that intermediate sized / aged females showed strongest preferences, other studies found that younger females are more selective (Ligout et al. 2012; Moore & Moore 2001). One explanation for this non-linear pattern of variation is that different sources of selection act on female preferences over their lifespan, i.e., similar preferences may have different causes. For example, experience-mediated expression of preferences is increasingly documented (Fowler-Finn

& Rodriguez 2012; Hebets 2003; Svensson et al. 2010), and young female treefrogs may have low responsiveness and selectivity because they are inexperienced. By contrast, old females may have low responsiveness and selectivity because they are showing signs of senescence (Moore & Moore 2001).

### **Effect of condition on female preferences**

Body condition is the quality measure most commonly used to investigate variation in preferences (see above), probably because of the straightforward prediction that if mate preferences are costly, then females with more energy reserves (i.e., better condition) should be able to better bear this cost (Alem & Greenfield 2010; Cotton et al. 2006; Iwasa & Pomiankowski 1991; Kokko et al. 2002). Female gray treefrogs indeed did show an effect of body condition on call duration preference, namely in the tolerance for call duration. Overall, females preferred longer calls. However, the shape of the call duration preference function suggests that this preference is best viewed not as a preference for long calls, but a discrimination against short calls. The function falls off steeply towards the low end, indicating that the strongest discrimination occurs between very short and intermediate duration calls. Interestingly, extremely low condition and extremely high condition females were significantly less tolerant of calls of very low duration, while females of intermediate body condition were the most tolerant with a large proportion of that group being tolerant of the entire testing range. Thus, again I did not find the predicted linear relationship between condition and preference, but a pattern in which low and high quality individuals show similar preferences. Again, different causes may be responsible for similar preferences. On the one hand, low condition females may try to

mate with the best quality male (with the longest call), because they do not have sufficient energy reserves for a second clutch and thus must make their one opportunity for reproduction count. High quality females may be more able to burden the cost of being more selective.

Previous studies on gray treefrog female preferences have also documented a discrimination against very short calls rather than a preference for extremely long ones (Gerhardt 1991; Gerhardt & Brooks 2009; Gerhardt et al. 1996; Gerhardt & Schul 1999). A novel and important insight from the present study is that this is not a general preference shown by every female, but an emergent pattern arising from individual of different condition showing different preferences.

### **Effect of fecundity on female preferences**

Fecundity (clutch size) had no significant relationship to any preference measured for pulse rate or call duration. This is a surprising result given the large amount of variation in clutch size, combined with its direct relationship to reproductive investment. Although this measure of “direct investment” showed no relationship to call trait preferences, alternative measures such as relative egg size should be addressed in future research. Egg size may vary within and between clutches (Berven & Chadra 1988; Kaplan & King 1997), and there may be trade-offs between number and size of eggs in a clutch (Berven & Chadra 1988). Larger eggs result in shorter larval development time (Berven & Chadra 1988; Cherdantseva et al. 2007; Ficetola et al. 2011), and a better measure of reproductive investment may have been to assess the size of a female’s eggs, not their number.

### **Is species recognition or conspecific mate choice more strongly affected by female quality?**

I had predicted that there will be a tighter correlation between female quality and preference for longer duration calls (conspecific mate quality) than to calls of the correct pulse rate (species recognition). I found support for this prediction: pulse rate preferences were only affected by one quality trait (SVL, potentially indicating age and experience), while call duration preferences were influenced by two quality traits (condition and SVL). This suggests that species recognition is somewhat more immune to quality effects than choice for conspecific mate quality.

### **Implications for sexual selection**

Females preferred trait values for both call duration and pulse rate that were higher than what the majority of males in this population are producing, suggesting that there is currently weak directional selection towards longer calls and higher pulse rates. Peak preferences were not related to quality for either call trait, indicating that this directional selection is independent of female quality. However, the strength with which these traits are selected for does have some relationship to female quality (size and body condition).

Response effort was the preference function trait with the strongest link to female quality. Given the anuran mating system, in which the long handling time associated with amplexus and oviposition means that males can only mate once per night, responsive females may play a disproportionately important role in sexual selection. Females that respond fastest have the best chances of mating with the male of their choice, and males with call traits preferred by those fast females are predicted to have highest mating



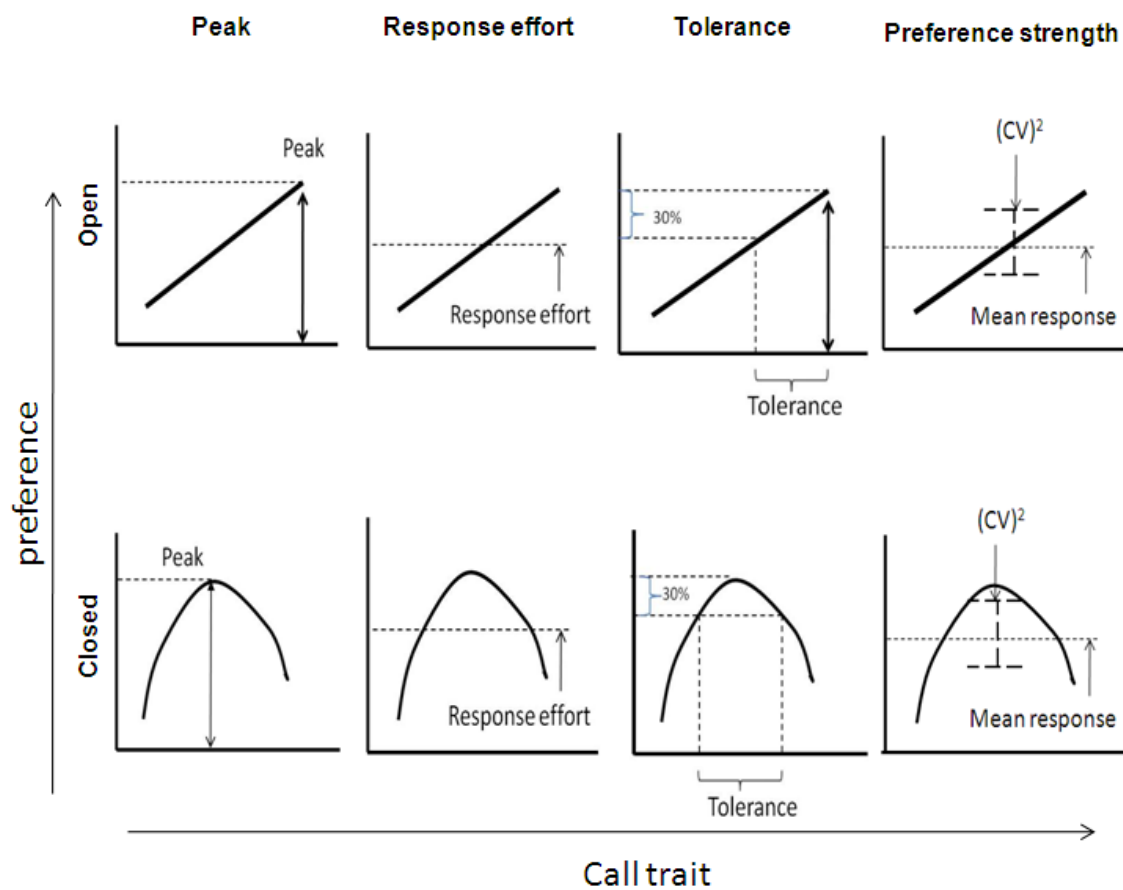
success and thus influence the call trait distribution in the next generation. An important finding of my study is that the group of females responding fastest is the least selective group, while the group of females responding slowest shows the strongest preferences. This apparent trade-off between responsiveness and selectivity has important consequences for sexual selection, because it should weaken selection on male call traits, and thus allow for the maintenance of variation in male traits in the population.

What is the underlying cause of the observed negative correlation between responsiveness and selectivity? One potential scenario may be that the trade-off arises from quality-mediated differences in the expressed phenotype, i.e., that low quality induces higher selectivity, while intermediate quality induces higher responsiveness. Alternatively, both aspects of the female preference may be linked and arise from physiological constraints of the task of mate selection. For example, a highly selective female may spend more time carefully assessing male calls, and consequently approach the source more slowly. By contrast, a less selective female may spend less time in call assessment and can therefore approach the caller more quickly.

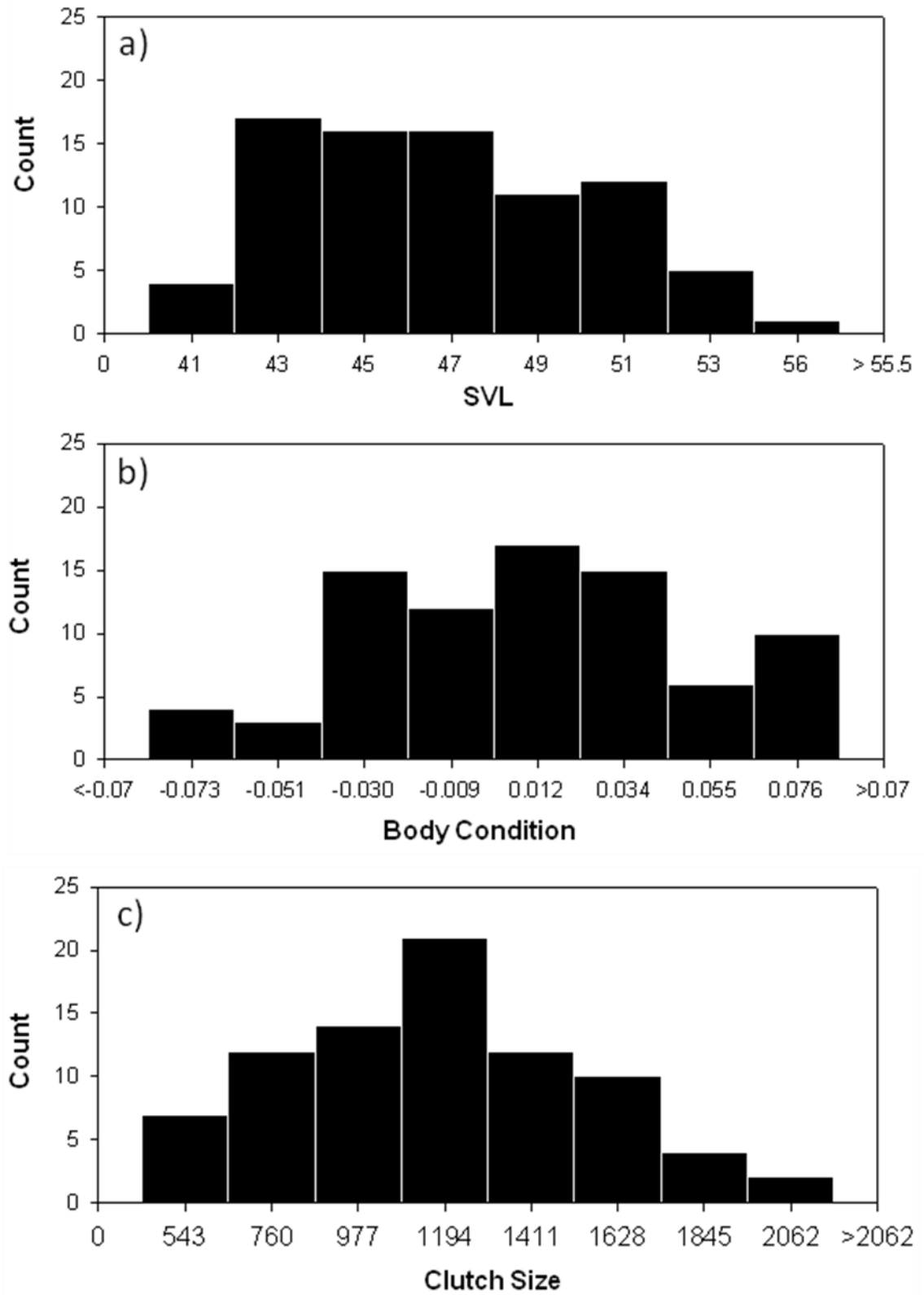
Because female quality showed at least some effect on female preferences, ecological factors have the potential to affect sexual selection in this species. In years with favourable conditions for growth/survival and energy accumulation, high quality individuals should make up a larger proportion of the mate searching female population, and because of their higher selectivity, sexual selection for call traits should increase. A similar pattern is expected for years with unfavourable conditions, which should increase the proportion of low quality individuals that nevertheless show stronger selectivity in their preferences. In average years, the resulting higher proportion of intermediate quality

individuals with low selectivity should result in relaxed sexual selection. This, too, should result in the maintenance of variation, but on a different time scale. It would be interesting to see if the distribution of male call traits in the population fluctuates over time and in accordance with ecological conditions. Documenting such a pattern might be difficult, though, because the several-year life-span of male tree frogs probably leads to an overlap of age classes, thus washing out any predicted pattern of fluctuating among-year variation in calls.

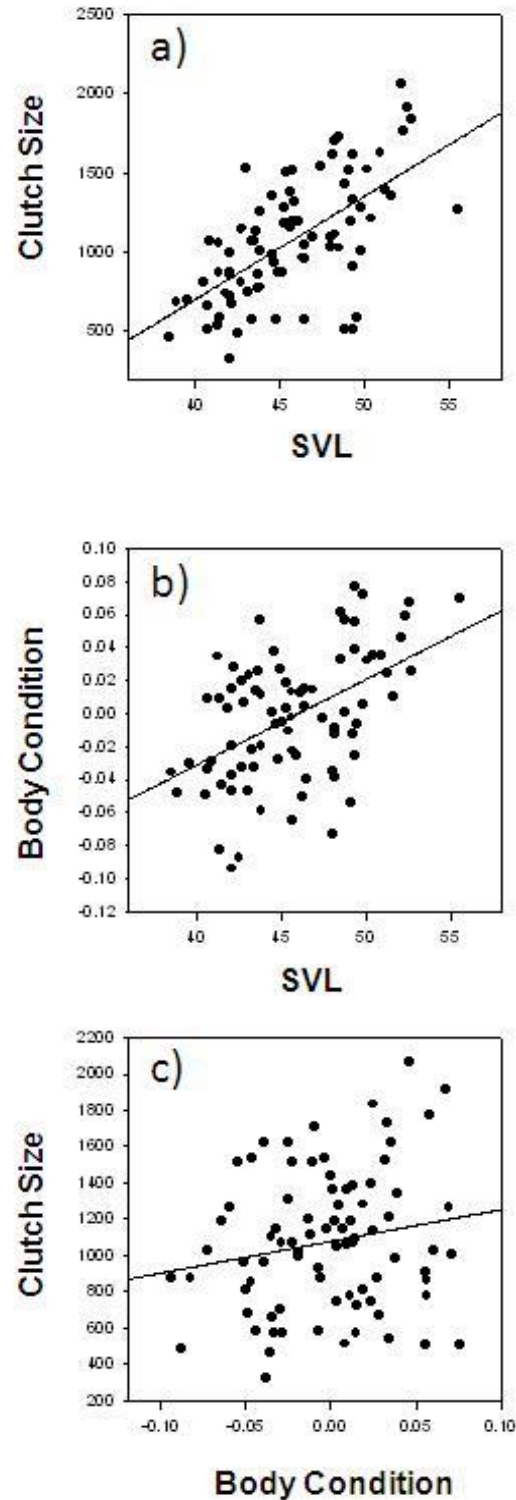
## FIGURE AND FIGURE LEGENDS



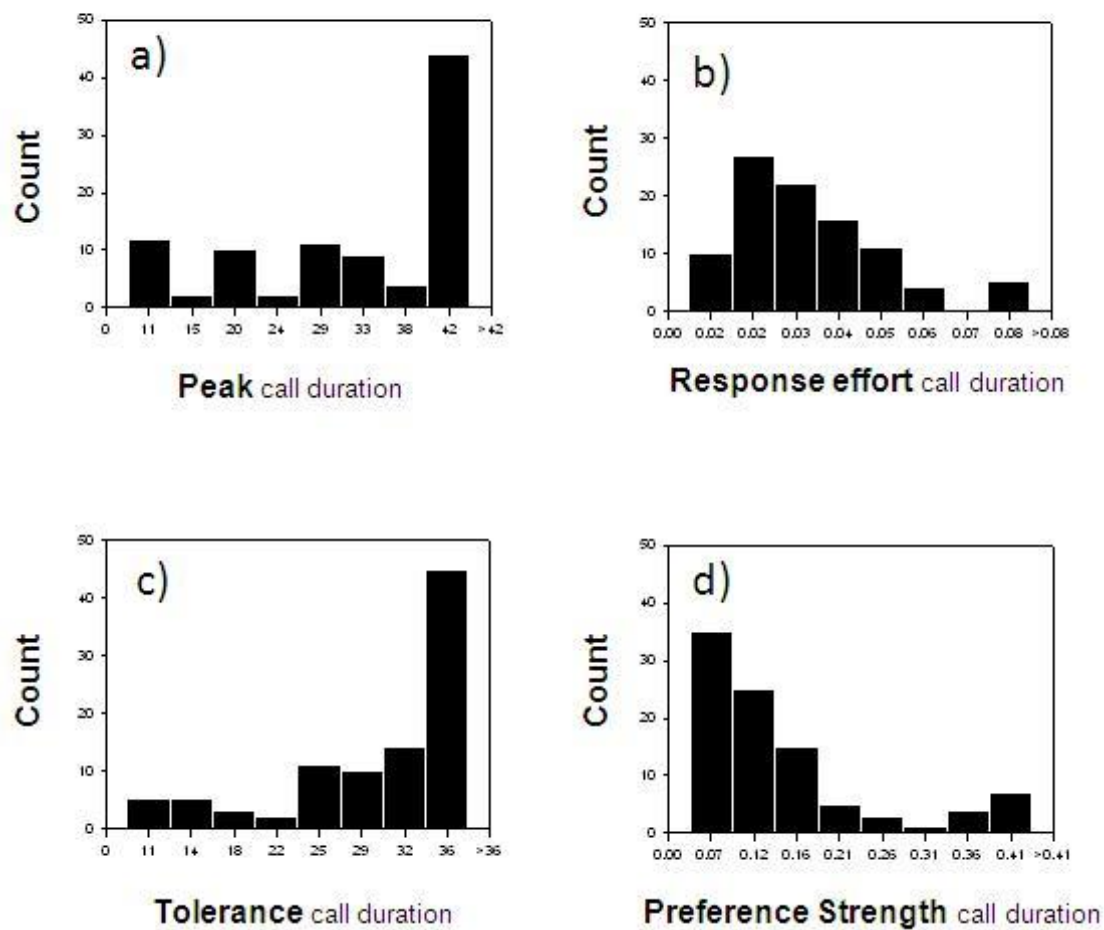
**Figure 1:** Preference function metrics: Peak; a measure of the call trait with the strongest response, Response effort; a measure of the average response across all call traits measured, Tolerance; the range within the continuum of male traits that a female will respond to, measured as the width of the preference at 70% of the peak response and Preference strength; the difference in responsiveness between the favorite stimuli and least favorite stimuli, measured as the squared coefficient of variation in responses across all call traits, for an open functions (top) and closed functions (bottom).



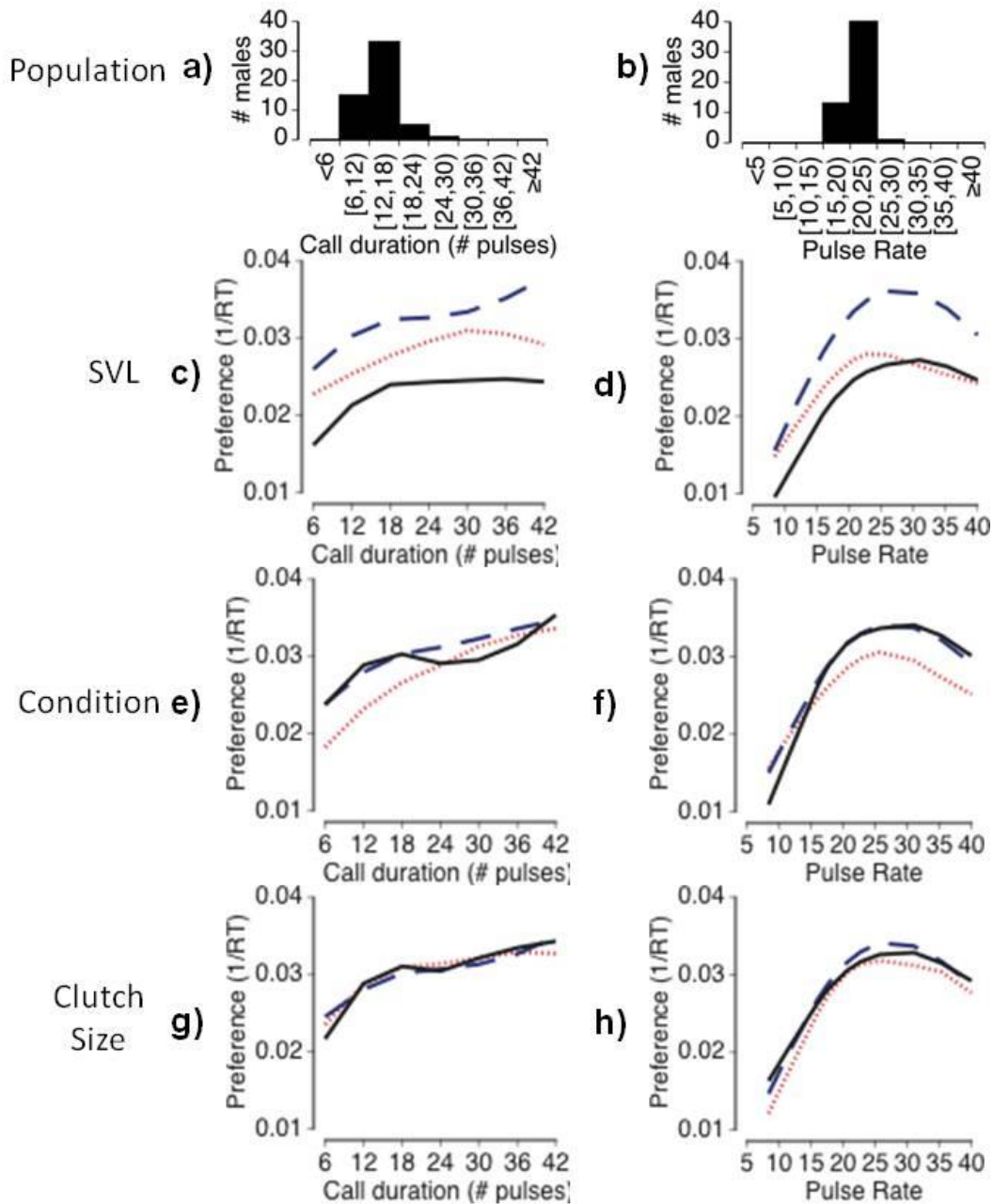
**Figure 2:** Distribution of female quality measures in terms of a) SVL, b) condition index and c) clutch size (N=82).



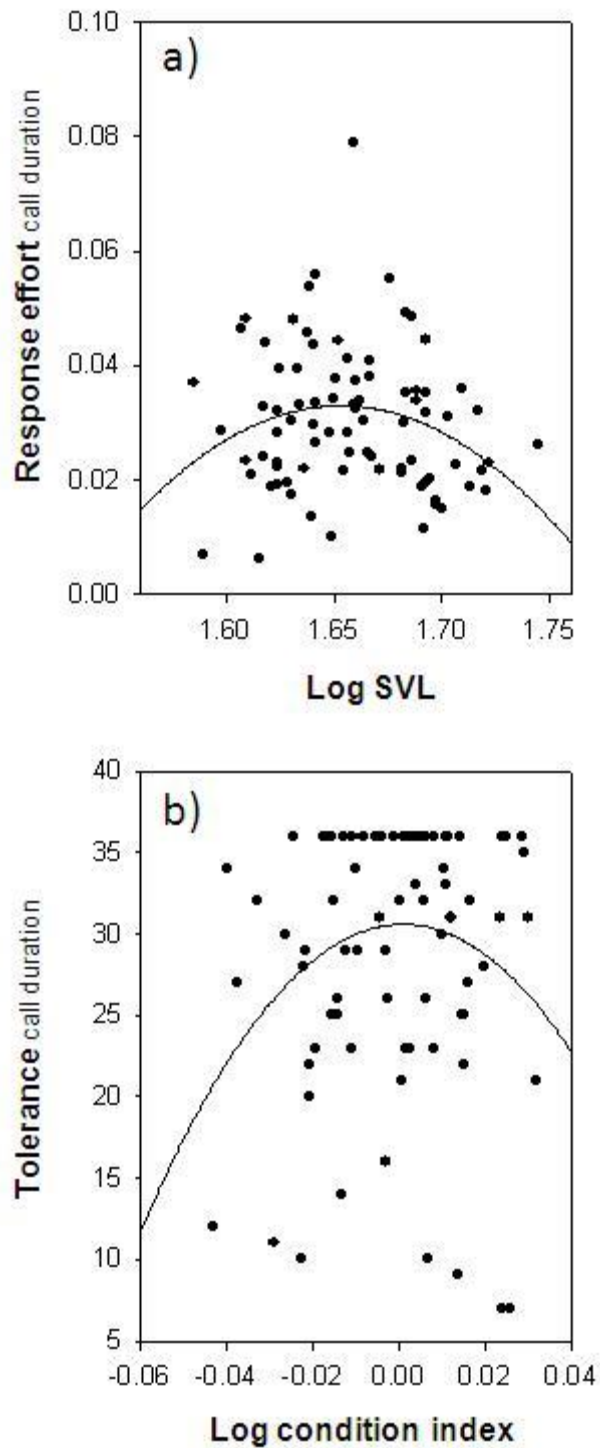
**Figure 3:** Correlation of quality measures a) SVL Vs. Clutch size ( $F_{1, 81} = 52.14$   $P < 0.0001$ ) b) condition Vs. clutch size ( $F_{1, 81} = 2.67$   $P < 0.11$ ) and c) SVL Vs. condition ( $F_{1, 81} = 24.71$   $P < 0.0001$ ). SVL was strongly correlated to both condition index and clutch size.



**Figure 4:** Distribution of preference function traits for call duration a) peak b) response effort c) tolerance and d) preference strength (N=82).

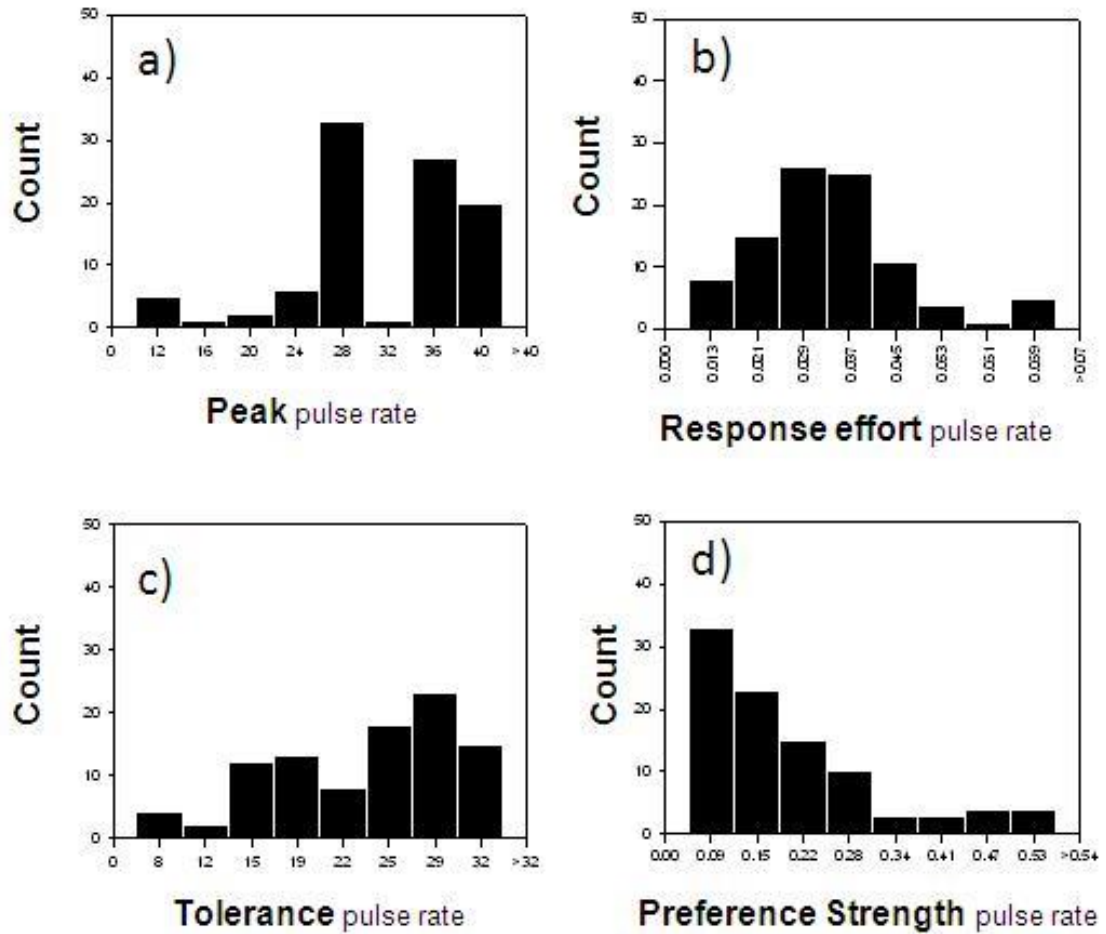


**Figure 5:** Distribution of male calls sampled for a) call duration and b) pulse rate. Female average preference functions by condition (High = black solid line, Medium = blue large dashed line, Low = red small dotted line), grouped by mean  $\pm$  1 standard deviation being medium and above and below respectively the high and low groups. SVL ( $n=13$  high, 57 medium, 12 low) for c) call duration and d) pulse rate. Clutch size ( $n=15$  high, 52 medium, 15 low) for e) call duration and f) pulse rate. Body Condition ( $n=12$  high, 57 medium, 13 low) for g) call duration and h) pulse rate.

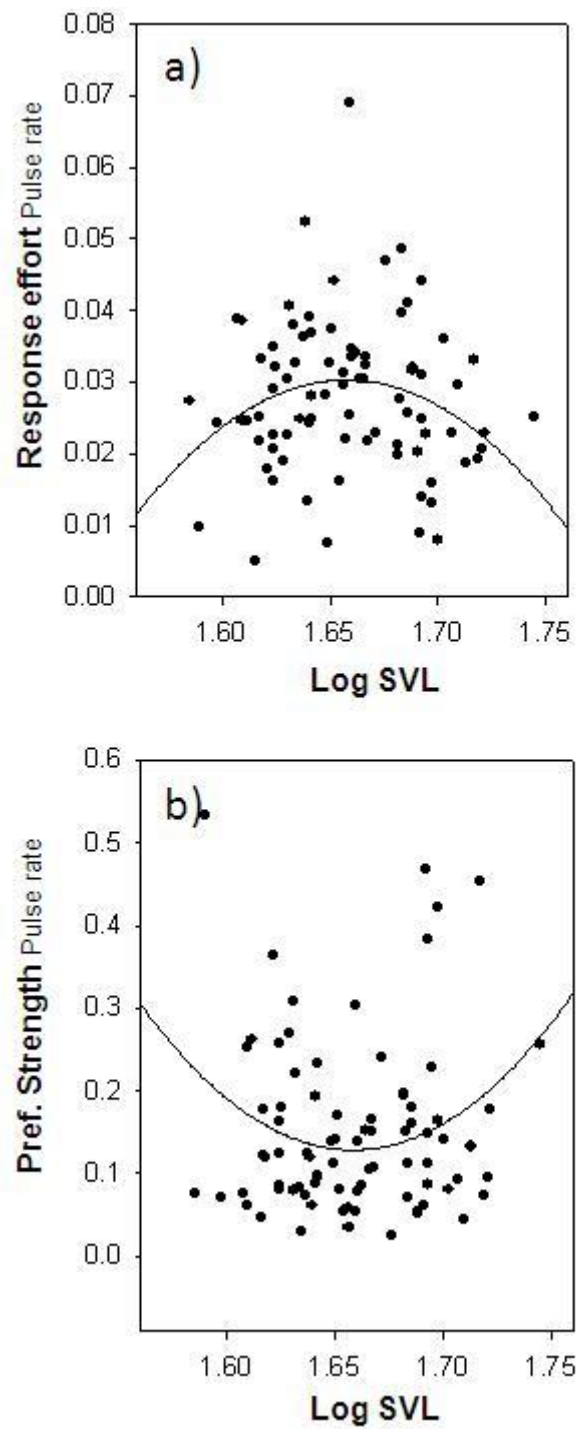


**Figure 6:** Significant interactions between call duration response variables and quality measures. a) Individuals of intermediate SVL had higher response efforts b) individuals of intermediate condition had larger tolerances.

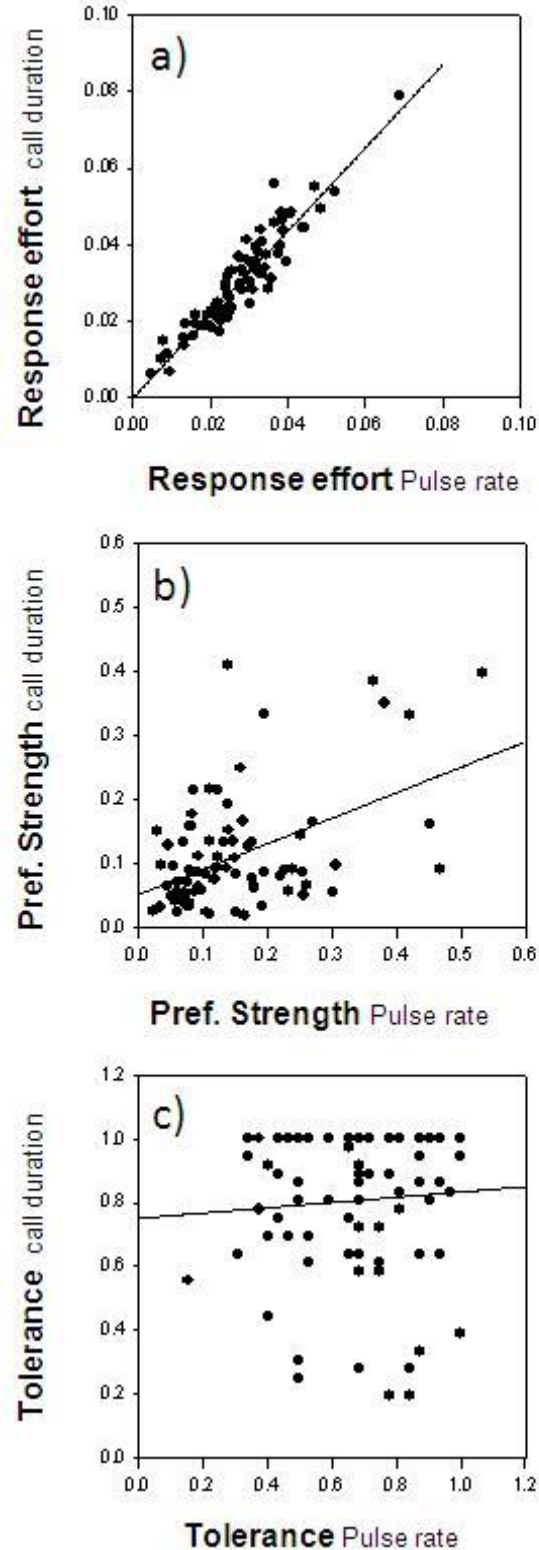




**Figure 7:** Distributions of preference function traits for pulse rate a) peak b) response effort c) tolerance and d) preference strength (N=82).



**Figure 8:** Significant interactions of pulse rate response variables with quality measures. a) individuals with intermediate SVL had higher response effort b) individuals with intermediate SVL had weakest preference strengths.



**Figure 9:** Correlation of female preference traits across call stimuli. Female a) response effort was strongly correlated ( $F_{1,81} = 566.7$ ,  $P < 0.0001$ ,  $R^2 = .87$ ) as was b) preference strength ( $F_{1,81} = 23.1$ ,  $P < 0.0001$ ,  $R^2 = .21$ ) however c) tolerance ( $F_{1,81} = .41$ ,  $P < .5217$ ,  $R^2 = 0.00$ ) was not across duration and pulse rate trials.

## TABLE AND TABLE LEGENDS

**Table 1:** Analysis of responses of gray treefrog females (N=82), testing for the effect of female quality on responses to variation in call duration. Significant P-values are highlighted in bold.

| <b>Sources of Variation</b> |                                 | <b>df</b>     | <b>F ratio</b> | <b>P<sub>≪</sub></b> |
|-----------------------------|---------------------------------|---------------|----------------|----------------------|
| <b>SVL</b>                  |                                 |               |                |                      |
|                             | <b>Stimuli</b>                  | <b>1, 481</b> | <b>56.8476</b> | <b>&lt;0.0001</b>    |
|                             | SVL                             | 1, 79         | 0.4445         | 0.5069               |
|                             | Stimuli x Stimuli               | 1, 481        | 2.8891         | 0.0898               |
|                             | <b>SVL x SVL</b>                | <b>1, 79</b>  | <b>4.3455</b>  | <b>0.0403</b>        |
|                             | Stimuli x SVL                   | 1, 481        | 1.0338         | 0.3098               |
| <b>Body Condition</b>       |                                 |               |                |                      |
|                             | <b>Stimuli</b>                  | <b>1, 481</b> | <b>57.0037</b> | <b>&lt;0.0001</b>    |
|                             | Body condition                  | 1, 79         | 0.1124         | 0.7384               |
|                             | Stimuli x Stimuli               | 1, 481        | 2.8486         | 0.0921               |
|                             | Body condition x Body condition | 1, 79         | 3.2175         | 0.0767               |
|                             | <b>Stimuli x Body condition</b> | <b>1, 481</b> | <b>4.7938</b>  | <b>0.029</b>         |
| <b>Clutch size</b>          |                                 |               |                |                      |
|                             | <b>Stimuli</b>                  | <b>1,481</b>  | <b>56.6</b>    | <b>&lt;0.0001</b>    |
|                             | Clutch size                     | 1,79          | 0.002          | 0.9641               |
|                             | Stimuli x Stimuli               | 1,481         | 2.923          | 0.088                |
|                             | Clutch size x clutch size       | 1,79          | 0.2790         | 0.5989               |
|                             | Stimuli x clutch size           | 1,481         | 0.1545         | 0.6944               |

**Table 2:** Clutch size did not affect preference traits for call duration, but females of different SVL and condition showed differences in response effort and tolerance (condition only). Female quality never affected peak preference or preference strength. Significant P-values are highlighted in bold.

| Quality measure       | Preference trait       | Linear    |         |          | Quadratic       |              |               |
|-----------------------|------------------------|-----------|---------|----------|-----------------|--------------|---------------|
|                       |                        | Std Error | t ratio | Prob > t | Std Error       | t ratio      | Prob > t      |
| <b>SVL</b>            | Peak                   | 41.35614  | 0.43    | 0.6687   | 1053.247        | -1.27        | 0.2068        |
|                       | <b>Response effort</b> | 0.039323  | -0.58   | 0.5636   | <b>1.002977</b> | <b>-2.12</b> | <b>0.0374</b> |
|                       | Tolerance              | 26.53564  | 0.52    | 0.6029   | 676.8247        | 0.36         | 0.723         |
|                       | Preference strength    | 0.287144  | -0.23   | 0.8148   | 7.323977        | 1.44         | 0.1528        |
| <b>Body Condition</b> | Peak                   | 84.44092  | -1.24   | 0.2184   | 3957.78         | -0.13        | 0.8943        |
|                       | Response effort        | 0.080743  | -0.38   | 0.7046   | 3.806268        | -1.79        | 0.0769        |
|                       | <b>Tolerance</b>       | 52.43049  | 0.35    | 0.7273   | <b>2471.606</b> | <b>-2.07</b> | <b>0.0415</b> |
|                       | Preference strength    | 0.578994  | -0.83   | 0.4116   | 27.29411        | 1.40         | 0.1655        |
| <b>Clutch size</b>    | Peak                   | 9.210486  | 0.75    | 0.456    | 41.75834        | -0.02        | 0.983         |
|                       | Response effort        | 0.009003  | 0.02    | 0.982    | 0.040639        | -0.48        | 0.6315        |
|                       | Tolerance              | 5.783695  | 1.79    | 0.0769   | 26.10778        | 1.2          | 0.2338        |
|                       | Preference strength    | 0.064586  | -0.30   | 0.7635   | 0.291543        | -0.19        | 0.8463        |

**Table 3:** Analysis of responses of gray treefrog females (N=82), testing for the effect of female quality on responses to variation in pulse rate. Significant P-values are highlighted in bold.

| <b>Sources of Variation</b>     | <b>df</b>     | <b>F ratio</b>  | <b>P<math>\leq</math></b> |
|---------------------------------|---------------|-----------------|---------------------------|
| <b>SVL</b>                      |               |                 |                           |
| <b>Stimuli</b>                  | <b>1, 481</b> | <b>200.0983</b> | <b>&lt;0.0001</b>         |
| SVL                             | 1, 79         | 0.0001          | 0.9921                    |
| <b>Stimuli x Stimuli</b>        | <b>1, 481</b> | <b>145.7532</b> | <b>&lt;0.0001</b>         |
| <b>SVL x SVL</b>                | <b>1, 79</b>  | <b>5.4195</b>   | <b>0.0225</b>             |
| Stimuli x SVL                   | 1, 481        | 1.2239          | 0.2689                    |
| <b>Body Condition</b>           |               |                 |                           |
| <b>Stimuli</b>                  | <b>1, 481</b> | <b>200.5016</b> | <b>&lt;0.0001</b>         |
| Body condition                  | 1, 79         | 0               | 0.999                     |
| <b>Stimuli x Stimuli</b>        | <b>1, 481</b> | <b>145.7757</b> | <b>&lt;0.0001</b>         |
| Body condition x Body condition | 1, 79         | 3.4597          | 0.0666                    |
| Stimuli x Body condition        | 1, 481        | 1.9678          | 0.1611                    |
| <b>Clutch size</b>              |               |                 |                           |
| <b>Stimuli</b>                  | <b>1, 481</b> | <b>199.3071</b> | <b>&lt;0.0001</b>         |
| Clutch size                     | 1, 79         | 0.0721          | 0.789                     |
| <b>Stimuli x Stimuli</b>        | <b>1, 481</b> | <b>145.0577</b> | <b>&lt;0.0001</b>         |
| Clutch size x clutch size       | 1, 79         | 0.2117          | 0.6467                    |
| Stimuli x clutch size           | 1, 481        | 0.5401          | 0.4626                    |

**Table 4:** Clutch size did not affect preference traits for pulse rate, but females of different SVL and condition showed differences in response effort and preference strength (SVL only). Female quality never affected peak preference or tolerance. Significant P-values are highlighted in bold.

| Quality measure       | Preference trait           | Linear    |         |          | Quadratic       |              |               |
|-----------------------|----------------------------|-----------|---------|----------|-----------------|--------------|---------------|
|                       |                            | Std Error | t ratio | Prob > t | Std Error       | T ratio      | Prob > t      |
| <b>SVL</b>            | Peak                       | 24.6726   | 1.55    | 0.1265   | 629.3055        | -1.68        | 0.0977        |
|                       | <b>Response effort</b>     | 0.033765  | -0.1    | 0.9223   | <b>0.861208</b> | <b>-2.31</b> | <b>0.0237</b> |
|                       | Tolerance                  | 20.48688  | -0.06   | 0.9543   | 522.5435        | 0.04         | 0.9646        |
|                       | <b>Preference strength</b> | 0.33553   | 0.05    | 0.9629   | <b>8.558116</b> | <b>2.14</b>  | <b>0.0358</b> |
| <b>Body Condition</b> | Peak                       | 51.43234  | 0.39    | 0.6977   | 2424.552        | -0.2         | 0.8455        |
|                       | Response effort            | 0.069279  | -0.14   | 0.8875   | 3.265859        | -1.89        | 0.0624        |
|                       | Tolerance                  | 41.44052  | 0.69    | 0.4933   | 1953.532        | -0.01        | 0.9916        |
|                       | Preference strength        | 0.698258  | -0.71   | 0.4794   | 32.91629        | 0.03         | 0.9743        |
| <b>Clutch size</b>    | Peak                       | 5.595809  | 1.1     | 0.2728   | 25.25965        | 0.33         | 0.7439        |
|                       | Response effort            | 0.007727  | 0.33    | 0.7453   | 0.03488         | -0.53        | 0.5988        |
|                       | Tolerance                  | 4.461586  | -0.23   | 0.8149   | 20.13974        | -1.73        | 0.0867        |
|                       | Preference strength        | 0.076132  | -0.31   | 0.7610   | 0.343663        | 1.09         | 0.2799        |

## REFERENCES

- Ahuja, A., De Vito, S. & Singh, R. S. 2011 Condition dependence and the nature of genetic variation for male sex comb bristle number in *Drosophila melanogaster*. *Genetica* 139, 505-510.
- Alem, S. & Greenfield, M. D. 2010 Economics of mate choice at leks: do female waxmoths pay costs for indirect genetic benefits? *Behavioral Ecology* 21, 615-625.
- Anderson, M. 1994 *Sexual Selection*: Princeton Univ. Press, Princeton.
- Anjos-Duarte, C. S., Costa, A. M. & Joachim-Bravo, I. S. 2011 Influence of Female Age on Variation of Mate Choice Behavior in Mediterranean Fruit Fly (Diptera: Tephritidae). *Journal of Insect Behavior* 24, 11-21.
- Bailey, N. W. 2008 Love will tear you apart: different components of female choice exert contrasting selection pressures on male field crickets. *Behavioral Ecology* 19, 960-966.
- Bakker, T. C. M., Kunzler, R. & Mazzi, D. 1999 Sexual selection - Condition-related mate choice in sticklebacks. *Nature* 401, 234-234.
- Baldauf, S. A., Engqvist, L., Ottenheym, T., Bakker, T. C. M. & Thunken, T. 2013 Sex-specific conditional mating preferences in a cichlid fish: implications for sexual conflict. *Behavioral Ecology and Sociobiology* 67, 1179-1186.
- Baugh, A. T. & Ryan, M. J. 2009 Female tungara frogs vary in commitment to mate choice. *Behavioral Ecology* 20, 1153-1159.
- Berven, K. & Chadra, B. 1988 The relationship among egg size, density and food level on larval development in the wood frog (*Rana sylvatica*). *Oecologia* 75, 67-72.
- Booksmythe, I., Detto, T. & Backwell, P. R. Y. 2008 Female fiddler crabs settle for less: the travel costs of mate choice. *Animal Behaviour* 76, 1775-1781.
- Bos, D. H., Williams, R. N., Gopurenko, D., Bulut, Z. & Dewoody, J. A. 2009 Condition-dependent mate choice and a reproductive disadvantage for MHC-divergent male tiger salamanders. *Molecular Ecology* 18, 3307-3315.
- Cherdantseva, E. M., Cherdantsev, V. G. & Lyapkov, S. A. 2007 The influence of egg size on the intensity and duration of *Rana arvalis* metamorph development in an experiment performed in a spawning water body. *Zoologicheskyy Zhurnal* 86, 329-339.
- Coleman, S. W., Patricelli, G. L. & Borgia, G. 2004 Variable female preferences drive complex male displays. *Nature* 428, 742-745.



- Cotton, S., Rogers, D. W., Small, J., Pomiankowski, A. & Fowler, K. 2006a Variation in preference for a male ornament is positively associated with female eyespan in the stalk-eyed fly *Diasemopsis meigenii*. *Proceedings of the Royal Society B-Biological Sciences* 273, 1287-1292.
- Cotton, S., Small, J. & Pomiankowski, A. 2006b Sexual selection and condition-dependent mate preferences. *Current Biology* 16, R755-R765.
- Doty, G. V. & Welch, A. M. 2001 Advertisement call duration indicates good genes for offspring feeding rate in gray tree frogs (*Hyla versicolor*). *Behavioral Ecology and Sociobiology* 49, 150-156.
- Engqvist, L. 2009 Should I stay or should I go? Condition- and status-dependent courtship decisions in the scorpionfly *Panorpa cognata*. *Animal Behaviour* 78, 491-497.
- Ficetola, G. F., Visaggi, B., Bonardi, A., Padoa-Schioppa, E. & De Bernardi, F. 2011 Starting size and tadpole performance in the frog *Rana latastei*. *Journal of Zoology* 284, 15-20.
- Fowler-Finn, K. D. & Rodriguez, R. L. 2012 EXPERIENCE-MEDIATED PLASTICITY IN MATE PREFERENCES: MATING ASSURANCE IN A VARIABLE ENVIRONMENT. *Evolution* 66, 459-468.
- Fowler-Finn, K. D. & Rodriguez, R. L. 2013 Repeatability of mate preference functions in *Enchenopa* treehoppers (Hemiptera: Membracidae). *Animal Behaviour* 85, 493-499.
- Gerhardt, H. C. 1978 Temperature coupling in the vocal communication system of the gray treefrog *Hyla versicolor*. *Science* 199, 992-994.
- Gerhardt, H. C. 1991 Female Mate Choice in Treefrogs - Static and Dynamic Acoustic Criteria. *Animal Behaviour* 42, 615-635.
- Gerhardt, H. C. 1994 The evolution of vocalization in frogs and toads. *Annual Review of Ecology and Systematics* 25, 293-324.
- Gerhardt, H. C. & Brooks, R. 2009 Experimental Analysis of Multivariate Female Choice in Gray Treefrogs (*Hyla Versicolor*): Evidence for Directional and Stabilizing Selection. *Evolution* 63, 2504-2512.
- Gerhardt, H. C., Dyson, M. L. & Tanner, S. D. 1996 Dynamic properties of the advertisement calls of gray tree frogs: Patterns of variability and female choice. *Behavioral Ecology* 7, 7-18.
- Gerhardt, H. C. & Schul, J. 1999 A quantitative analysis of behavioral selectivity for pulse rise-time in the gray treefrog, *Hyla versicolor*. *Journal of Comparative Physiology a-Sensory Neural and Behavioral Physiology* 185, 33-40.

- Griggio, M. & Hoi, H. 2010 Only females in poor condition display a clear preference and prefer males with an average badge. *Bmc Evolutionary Biology* 10, -.
- Hale, M. L., Verduijn, M. H., Moller, A. P., Wolff, K. & Petrie, M. 2009 Is the peacock's train an honest signal of genetic quality at the major histocompatibility complex? *Journal of Evolutionary Biology* 22, 1284-1294.
- Halliday, T. R. & Verrell, P. A. 1988 Body Size and Age in Amphibians and Reptiles. *Journal of Herpetology* 22, 253-265.
- Hebets, E. A. 2003 Subadult experience influences adult mate choice in an arthropod: Exposed female wolf spiders prefer males of a familiar phenotype. *Proceedings of the National Academy of Sciences of the United States of America* 100, 13390-13395.
- Hebets, E. A., Wesson, J. & Shamble, P. S. 2008 Diet influences mate choice selectivity in adult female wolf spiders. *Animal Behaviour* 76, 355-363.
- Hedrick, A. V. & Dill, L. M. 1993 Mate Choice by Female Crickets Is Influenced by Predation Risk. *Animal Behaviour* 46, 193-196.
- Hedrick, A. V. & Kortet, R. 2012 Effects of body size on selectivity for mating cues in different sensory modalities. *Biological Journal of the Linnean Society* 105, 160-168.
- Holveck, M. J. & Riebel, K. 2010 Low-quality females prefer low-quality males when choosing a mate. *Proceedings of the Royal Society B-Biological Sciences* 277, 153-160.
- Howard, R. D. & Young, J. R. 1998 Individual variation in male vocal traits and female mating preferences in *Bufo americanus*. *Animal Behaviour* 55, 1165-1179.
- Hunt, J., Brooks, R. & Jennions, M. D. 2005 Female mate choice as a condition-dependent life-history trait. *American Naturalist* 166, 79-92.
- Iwasa, Y. & Pomiankowski, A. 1991 THE EVOLUTION OF COSTLY MATE PREFERENCES .2. THE HANDICAP PRINCIPLE. *Evolution* 45, 1431-1442.
- Jennions, M. D. & Petrie, M. 1997 Variation in mate choice and mating preferences: A review of causes and consequences. *Biological Reviews of the Cambridge Philosophical Society* 72, 283-327.
- Kaplan, R. H. & King, E. G. 1997 Egg size is a developmentally plastic trait: Evidence from long term studies in the frog *Bombina orientalis*. *Herpetologica* 53, 149-165.
- Kodric-Brown, A. & Nicoletto, P. F. 2001 Age and experience affect female choice in the guppy (*Poecilia reticulata*). *American Naturalist* 157, 316-323.

- Kokko, H., Brooks, R., McNamara, J. M. & Houston, A. I. 2002 The sexual selection continuum. *Proceedings of the Royal Society of London Series B-Biological Sciences* 269, 1331-1340.
- Kotiaho, J. S. 2000 Testing the assumptions of conditional handicap theory: costs and condition dependence of a sexually selected trait. *Behavioral Ecology and Sociobiology* 48, 188-194.
- Laucht, S. & Dale, J. 2012 CORRELATIONS OF CONDITION, TESTOSTERONE, AND AGE WITH MULTIPLE ORNAMENTS IN MALE HOUSE SPARROWS: PATTERNS AND IMPLICATIONS. *Condor* 114, 865-873.
- Lerch, A., Rat-Fischer, L., Gratier, M. & Nagle, L. 2011 Diet Quality Affects Mate Choice in Domestic Female Canary *Serinus canaria*. *Ethology* 117, 769-776.
- Lerch, A., Rat-Fischer, L. & Nagle, L. 2013 Condition-Dependent Choosiness For Highly Attractive Songs In Female Canaries. *Ethology* 119, 58-65.
- Ligout, S., Munier, D., Marquereau, L. & Greenfield, M. D. 2012 Chronological vs. Physiological Age as Determinants of Mating Decisions: Studies on Female Choice Over Lifespan in An Acoustic Moth. *Ethology* 118, 740-751.
- Lopez, S. 1999 Parasitized female guppies do not prefer showy males. *Animal Behaviour* 57, 1129-1134.
- Lykens, D. V. & Forester, D. C. 1987 Age Structure in the Spring Peeper - Do Males Advertise Longevity. *Herpetologica* 43, 216-223.
- Magnhagen, C. 1991 Predation Risk as a Cost of Reproduction. *Trends in Ecology & Evolution* 6, 183-185.
- Moore, P. J. & Moore, A. J. 2001 Reproductive aging and mating: The ticking of the biological clock in female cockroaches. *Proceedings of the National Academy of Sciences of the United States of America* 98, 9171-9176.
- Perrill, S. A. & Daniel, R. E. 1983 Multiple egg clutches in *Hyla regilla*, *H. cinerea* and *H. gratiosa*. *Copeia* 2, 513-516.
- Riebel, K., Naguib, M. & Gil, D. 2009 Experimental manipulation of the rearing environment influences adult female zebra finch song preferences. *Animal Behaviour* 78, 1397-1404.
- Rintamaki, P. T., Alatalo, R. V., Hoglund, J. & Lundberg, A. 1995 MATE SAMPLING BEHAVIOR OF BLACK GROUSE FEMALES (TETRAO TETRIX). *Behavioral Ecology and Sociobiology* 37, 209-215.
- Ritke, M. E., Babb, J. G. & Ritke, M. K. 1990 Life History of Gray Treefrog (*Hyla chrysoscelis*) in Western Tennessee. *Journal of Herpetology* 24, 135-141.

- Robinson, D. M. & Morris, M. R. 2010 Unraveling the complexities of variation in female mate preference for vertical bars in the swordtail, *Xiphophorus cortezi*. *Behavioral Ecology and Sociobiology* 64, 1537-1545.
- Rodriguez, R. L., Hallett, A. C., Kilmer, J. T. & Fowler-Finn, K. D. 2013 Curves as traits: genetic and environmental variation in mate preference functions. *Journal of Evolutionary Biology* 26, 434-442.
- Rodriguez, R. L., Ramaswamy, K. & Coccoft, R. B. 2006 Evidence that female preferences have shaped male signal evolution in a clade of specialized plant-feeding insects. *Proceedings of the Royal Society B-Biological Sciences* 273, 2585-2593.
- Sagor, E. S., Ouellet, M., Barten, E. & Green, D. M. 1998 Skeletochronology and geographic variation in age structure in the wood frog, *Rana sylvatica*. *Journal of Herpetology* 32, 469-474.
- Slagsvold, T. & Dale, S. 1991 MATE CHOICE MODELS - CAN COST OF SEARCHING AND COST OF COURTSHIP EXPLAIN MATING PATTERNS OF FEMALE PIED FLYCATCHERS. *Ornis Scandinavica* 22, 319-326.
- Slagsvold, T., Lifjeld, J. T., Stenmark, G. & Breiehagen, T. 1988 On the cost of searching for a mate in female pied flycatchers *Ficedula hypoleuca*. *Animal Behaviour* 36, 433-442.
- Svensson, E. I., Eroukhmanoff, F., Karlsson, K., Runemark, A. & Brodin, A. 2010 A ROLE FOR LEARNING IN POPULATION DIVERGENCE OF MATE PREFERENCES. *Evolution* 64, 3101-3113.
- Syriatowicz, A. & Brooks, R. 2004 Sexual responsiveness is condition-dependent in female guppies, but preference functions are not. *BMC Ecology* 4.
- Welch, A. M. 2000 What is good about "good genes" in gray tree frogs: how is call duration linked with larval quality? *American Zoologist* 40, 1253-1254.
- Welch, A. M., Gerhardt, H. C. & Semlitsch, R. D. 2002 Female preference strength and male call duration affect offspring fitness in gray tree frogs. *Integrative and Comparative Biology* 42, 1333-1333.
- Wells, K. D. 1976 Multiple egg clutches in the green frog (*Rana clamitans*). *Herpetologica* 32, 85-87.
- Wilgers, D. J. & Hebets, E. A. 2012 Age-related female mating decisions are condition dependent in wolf spiders. *Behavioral Ecology and Sociobiology* 66, 29-38.
- Woodgate, J. L., Bennett, A. T. D., Leitner, S., Catchpole, C. K. & Buchanan, K. L. 2010 Developmental stress and female mate choice behaviour in the zebra finch. *Animal Behaviour* 79, 1381-1390.