

Task differences confound sex differences in receiver permissiveness in túngara frogs

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In many mating systems, both sexes respond to the same sexual signal. In frogs, males typically call in response to advertisement calls, while females approach male calls in choosing a mate. The costs of signal detection errors are expected to differ between the sexes. Missed opportunities are costly for males because ignoring a signal results in failing to compete with rivals for mates, while their cost for misidentification is lower (time and energy displaying to the incorrect target). By contrast, for females, the cost of misidentification is high (mating with incorrect species or low-quality partner), while their cost for missed opportunity is lower because the operational sex ratio puts females at a premium. Consequently, females should be more selective in their response to signal variation than males. We report that presumed sexual differences in selectivity in túngara frogs (*Physalaemus pustulosus*) are task-specific rather than sex-specific. As predicted, male túngara frogs are less selective in their vocal responses than are females in their phonotactic responses. Males exhibiting phonotaxis to the same calls, however, are as selective as females, and are significantly more selective than when they respond vocally to the same calls. Our study shows that apparent differences between the sexes emerge from differences in the behaviours themselves and are not intrinsic to each sex. Analogous behavioural differences might confound sex differences in other systems; thus, we suggest consideration of the behavioural plasticity of sex as well as its stereotypy.

Keywords: mating signals; *Physalaemus pustulosus*; receiver permissiveness; sexual differences; sexual selection; signal selectivity

1. INTRODUCTION

In many species, males and females attend and respond to the same sexual signal produced by male conspecifics (reviewed in Berglund *et al.* 1996). While females use those signals during courtship and mate choice, males use them in competition with rival males. Theoretical and empirical studies indicate that the sexes are under different selective pressures to recognize and respond to sexual signals, and thus sex differences are expected (Searcy 1990). Two types of recognition errors can be made when responding to sexual signals: (i) missed opportunity, when an appropriate signal is falsely rejected as inappropriate (also known as type I error); and (ii) misidentification, when an inappropriate signal is falsely accepted as appropriate (also known as type II error). Based on the cost of recognition errors, Searcy & Brenowitz (1988) proposed that females should generally be more discriminating than males in their responses to sexual signals. Males responding to territorial intrusions or displays of competing males in a lek are under strong selection to avoid missed opportunities, since a male that ignores such signals may lose his territory, suffer cuckoldry or fail to attract a mate. There is, however, a lower cost for misidentification since such cost for males is restricted to the time and energy devoted to displaying to the incorrect target. By contrast, females are under strong selection to avoid misidentification (e.g. mating with the

wrong species or low-quality partner), while there is a lower cost for missed opportunities (e.g. being able to find a mate).

Evidence from avian studies confirms higher signal permissiveness in males than females in response to song variation (reviewed in Ratcliffe & Otter 1996). For example, red-winged blackbird (*Agelaius phoeniceus*) males do not distinguish between a mockingbird (*Mimus polyglottos*) imitation of red-winged blackbird song and a normal red-winged blackbird song, while females clearly discriminate between these songs, preferring the one produced by their own species (Searcy & Brenowitz 1988). Similarly, female swamp sparrows (*Melospiza georgiana*) respond preferentially to temporal patterns characteristic of the conspecific song (Searcy *et al.* 1981), while males do not show a preference (Peters *et al.* 1980). As predicted by Searcy (1990), sexual differences in species recognition extend beyond avian species; analogous differences between the sexes in their responses to sexual signals are also found in anurans. When the responses of male and female túngara frogs to 14 non-conspecific calls (species of the same genus and estimates of ancestral calls) were evaluated, males made more recognition errors than females (Bernal *et al.* 2007).

Comparisons of permissiveness to signal variation between the sexes are faced with a challenge: in response to sexual signals, males and females characteristically perform different behaviours. This is true in a variety of taxa, such as insects (Drosopoulos & Claridge 2006), fishes (Morris & Ryan 1996), frogs (Gerhardt & Huber 2002) and birds (Searcy 1992). In species using acoustic signals, for instance, males often respond to calls with their own calls, while females use such signals to locate and evaluate males.

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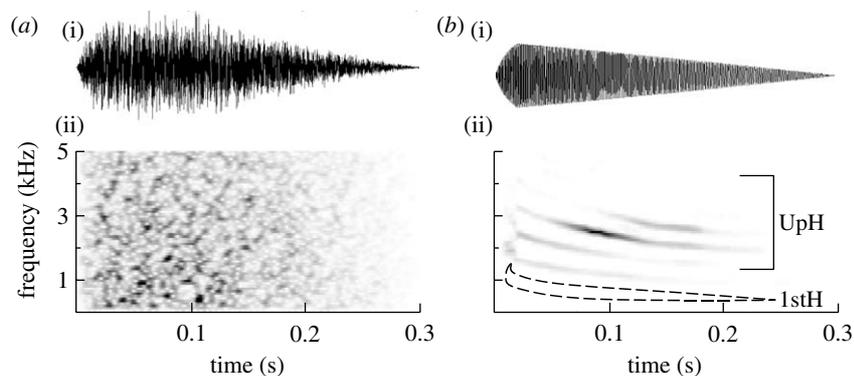


Figure 1. (i) Oscillograms and (ii) spectrograms of the synthetic túngara frog calls with altered frequency domain used to investigate the responses of the sexes to signal variation. (a) White noise filtered to match the mean amplitude envelope of the call and (b) call with the upper harmonics (UpH) only. The first harmonic, which contains approximately 50% of the energy of the call, is missing (1stH; dashed line).

Many studies of sexual differences have investigated the response of each sex to sexual signals, with the sexes performing different behaviours (Dabelsteen & Pedersen 1988; Searcy & Brenowitz 1988; Searcy 1990; Ratcliffe & Otter 1996; Bernal *et al.* 2007). Little attention has been given to the role of the behavioural output in signal permissiveness. The difference in behavioural tasks complicates direct comparisons between the sexes in permissiveness to sexual signals. The conundrum of sex and task differences occurs in many systems, obscuring an important question: is the difference between males and females in their permissiveness to sexual signals an intrinsic sexual difference or a difference in the task in which they are being evaluated? Here, we investigate the responses of males and females to variation in sexual signals when performing the same and different reproductive behaviours.

We investigate a Neotropical frog in which males produce calls intended to attract females and, at the same time, deter rival males. Male túngara frogs, *Physalaemus pustulosus*, aggregate to advertise at breeding ponds, drawing females and males to the chorus. At these aggregations, the sex ratio is skewed towards males at a ratio of approximately 3:1; thus, there is a surfeit of potential mates for all of the females, and many males never mate (Ryan 1985). Females use the male mating call to locate and assess mates. Her approach to the call, phonotaxis, indicates her decision. Males typically respond to calls of other males vocally, by calling back to them. Male túngara frogs, however, also perform phonotaxis (Ryan 1985, table 8.8; Marsh *et al.* 2000). Like males of many other species (Mountjoy & Lemon 1991; Kaspi & Yuval 1999; Pfenning *et al.* 2000; Bee 2007), male túngara frogs use the signals of other males to locate breeding sites. At dusk, males approach pools of water, attracted by calling males, reach the shore of the pool and skirt the shore edge in order to enter close to calling males. Brief physical interactions that involve kicking and production of aggressive calls occur when males are in close contact, but they quickly separate and begin producing advertisement calls. In túngara frogs, male phonotaxis is not involved in alternative mating strategies such as satellite behaviours (Perrill *et al.* 1978) or mate choice (Bush *et al.* 1996) as in some other anurans. Thus, in túngara frogs both sexes perform phonotaxis to sexual signals, while only males vocalize in response to the calls of other males.

In túngara frogs, females approaching calls and males calling back to calls show differences in permissiveness to variation in sexual signals (Bernal *et al.* 2007). Such apparent sexual differences, however, could be behaviour-specific and independent of sex. The same may be true in 'sex differences' in permissiveness to signal variation described in other species (e.g. Dabelsteen & Pedersen 1988; Searcy & Brenowitz 1988; Ratcliffe & Otter 1996). Attempts to contrast the sexes using procedures that do not rely on sex-specific behaviours have motivated studies using physiological measurements (Ikebuchi *et al.* 2003) and food-rewarded operant discrimination procedures (Weary 1992). In this study, we quantify the evoked vocal response of males, and the phonotaxis behaviour of both males and females to call variation, to test the alternative hypotheses that (i) differences in response are due to sex and are independent of behaviour, versus (ii) differences in response are due to behaviour and are independent of sex.

2. MATERIAL AND METHODS

Experiments were conducted in Gamboa, Panama, at the research facilities of the Smithsonian Tropical Research Institute. Túngara frogs were collected at breeding sites during the rainy season. Female frogs were collected in amplexus, while males were found either paired with females or calling at the ponds. We brought the frogs to the laboratory and tested them singly.

(a) *Experimental stimuli*

The mating calls of túngara frogs consist of a whine (a low-frequency sweep), which may be followed by up to seven secondary components called chucks. The whine is necessary and sufficient to elicit a behavioural response in females and males (Ryan 1985). We examined call recognition in response to the variants of the whine (without chucks). We explored call recognition altering specific parameters in the frequency domain of the signal. Frequency composition of mating calls is essential for call recognition in many species of anurans (Gerhardt & Huber 2002), including túngara frogs (Wilczynski *et al.* 1995). We generated synthetic versions of the calls that differed from the natural mating calls in their frequency domain in two ways: (i) synthetic calls lack the frequency structure found in the original calls, having instead the random power spectral density of white noise (figure 1a), and (ii) synthetic calls lack the first harmonic, which contains

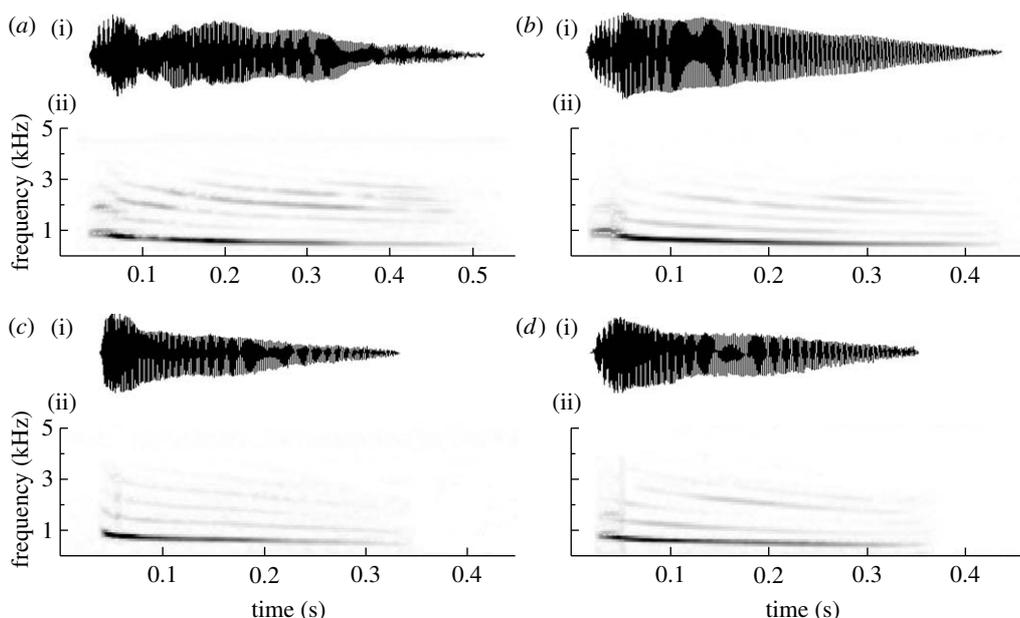


Figure 2. Natural túngara frog calls used to examine the responses of the sexes to signal variation encountered in the wild. Calls of (a) male A, (b) male B, (c) male C and (d) male D. (i) Oscillograms and (ii) spectrograms.

approximately 50 per cent of the energy of the call (figure 1*b*). To determine whether behavioural differences emerge in response to more subtle signal variation encountered in the wild, we also evaluated the responses of the sexes to natural calls (figure 2). We independently examined the effect of these signal variants on the response of both sexes in phonotaxis, and males in evoked vocal response.

We generated the synthetic stimuli by shaping sine waves using the software developed by J. Schwartz (Pace University, Pleasantville, NY; sample rate 20 kHz and 16 bit) using the mean values of the parameters of the calls in the population based on the recordings of 50 males analysed by Ryan & Rand (2003). Call parameters were calculated using batch processing programs in the software package SIGNAL (Engineering Design, Belmont, MA). Variables for constructing the synthetic stimuli were based on the mean values of a combination of the following eight spectral and temporal call parameters: *maximum frequency*, the maximum frequency of the whine's first harmonic; *final frequency*, the frequency of the first harmonic at the end of the call, which is always the lowest frequency; *call duration*, the duration of the whine; *rise time*, the time from the whine's onset to its maximum amplitude; *fall time*, the time from the whine's maximum amplitude to the end of the call; *whine shape*, the proportion of the call's duration from the onset to its mid-frequency; *rise shape*, the proportion of the call's duration from the onset of the call to half the maximum amplitude during the rise; and *fall shape*, the proportion of the call's duration from the maximum amplitude to half the maximum amplitude during the fall. Additional information on the recordings, call parameters and the synthesis procedure can be found in Ryan & Rand (1999).

We generated the 'whine-like noise' by synthesizing white noise, bandpass filtered to 0–10 kHz, and shaped to match the mean amplitude envelope of the túngara frog call in the study population. To synthesize the calls that varied in harmonic composition, we calculated the population average for each harmonic frequency of the whine by determining its 'contour', i.e. its frequency-by-time and amplitude-by-time variations. The mean contours for each harmonic

were then used to synthesize an average call for the population. A call including only the second, third, fourth and fifth harmonic frequencies (hereafter upper harmonics) was produced, adding the contours of harmonics two to five while maintaining their original relative amplitude. To examine the role of missing the first harmonic, excluding the potential effect of decreased amplitude due to not having this frequency component, we broadcast this call at the same peak amplitude as the other experimental stimuli.

We randomly chose the calls of four males from the same population where the test frogs were collected. These calls were recorded following the standard procedures using a Marantz PMD 420 recorder and a Sennheiser ME 80 microphone with K3U power module on a magnetic cassette tape. Air temperatures at the calling sites were within a few degrees of 25°C. The response to these natural calls was compared with the response to a burst of whine noise (bandpass filtered to 0–10 kHz, with the average duration of the whine).

(b) Phonotaxis

We tested female and male túngara frogs in two kinds of phonotaxis experiments: recognition and discrimination. In recognition experiments, we presented the frogs with an experimental stimulus (whine-like noise or whine missing the first harmonic) versus a burst of white noise, to determine whether túngara frogs recognize such variants of the whine. In discrimination experiments, we presented the frogs with a natural call versus a synthetic, average call. Our use of these terms is consistent with previous studies (Ryan & Rand 1995, 1999).

Túngara frogs were tested in a 1.8 × 2.7 m sound attenuation chamber (Acoustic Systems, Austin, TX). We broadcast the experimental stimuli antiphonally from a Dell computer through an amplifier and ADS speakers in the centre of walls opposite one another. The peak amplitude of the calls at the centre of the arena, where the frog was released, was 82 dB SPL (re. 20 μPa). The speakers were balanced for sound pressure level with a 500 Hz continuous tone. We used a GenRad sound level meter model 1982 (fast, linear weighting) to measure the sound pressure. Tests were

conducted under infrared light and the movement of the frog was monitored on a video monitor (outside the testing chamber) that received input from a wide lens video camera on the chamber's ceiling (Fuhrman Diversified, Inc., Houston, TX, USA). A response was scored when the frog approached a speaker within 10 cm, excluding the approaches along the walls of the arena. We scored a 'no response' if the frog either remained motionless for 5 min after being released, stopped moving for 2 min at any time during the experiment or did not approach any speaker in 15 min. To discern that an absence of response was due to lack of motivation rather than lack of attraction to the stimulus, we tested the frogs with calls known to elicit phonotaxis preceding and following the tests with the experimental stimuli. Only data from the frogs that responded in both tests, controlling for motivation, were included in the analysis. A complete description of the testing chamber and details of the protocol can be found in Ryan & Rand (1999). We tested 20 individuals per sex on each experiment, for a total of 240 choice tests.

To statistically test call recognition in phonotaxis for each stimulus, we performed an exact binomial test against an experimentally determined null hypothesis estimating the number of frogs that encounter a speaker without reference to the stimulus it is broadcasting (2 out of 20 females approach a silent speaker by chance; Ryan & Rand 1999). We determined the preference for a signal in phonotaxis using an exact binomial test for each pair of stimuli, contrasting the number of frogs approaching each stimulus in a test with a 1:1 expected ratio.

(c) *Evoked vocal response*

Calling male túngara frogs were tested in individual acoustically isolated chambers (30.5×46×30.5 cm; see also Bosch *et al.* 2002). Each male was placed in a plastic bag (previously shown to be acoustically transparent; Ryan & Rand 1998) inside the acoustic chamber, which contained a Radio Shack miniature microphone and a small, wide frequency range speaker (Cambridge SoundWorks Inc., Ensemble IV). We presented the experimental stimuli using a JVC XL-PG7 CD player through a Realistic SA-10 amplifier at 90 dB SPL (re. 20 µPa) at 0.5 m measured by a GenRad sound pressure level meter model 1982 (fast, linear weighting).

We stimulated the males to call by broadcasting a recording of a high-density túngara frog chorus and, once a male began to call, we initiated the playback experiments. Each test consists of a set of five 60 second intervals: (i) control stimulus (synthetic average whine), (ii) silence, (iii) experimental stimulus (whine-like noise, call with upper harmonics only or natural call), (iv) silence, and (v) control stimulus (synthetic average whine) (Ryan & Rand 1998; Bosch *et al.* 2002; Bernal *et al.* 2007). Only cases in which males called during both control stimuli were included in the analysis, to eliminate cases of no response due to lack of motivation. We performed a total of 78 evoked vocal response tests distributed as follows: whine-like noise, $n=20$ males; upper harmonics, $n=18$ males; and natural calls, $n=10$ males for each of the four calls (referred to as calls of male A, male B, male C, male D), for a total of 40 males.

In response to the experimental stimuli, males produced simple (whines only) and complex calls (whines followed by chucks). These two call components (whines and chucks) are correlated, but provide different information. Hence, we combined both measures to characterize the overall response

of males using the first component of a principal components analysis. We combined the total number of whines and chucks for each interval during the test (in all experiments PC1 explained more than 90.1% of the variation). We determined call recognition by contrasting the calling behaviour during the experimental stimulus with calling behaviour during silence before and after it, for each individual, using a Wilcoxon signed-ranked test following Bernal *et al.* (2007).

(d) *Comparison between the sexes*

To contrast the responses of calling males to those of females and males in phonotaxis, we converted the vocal response of males into a binary response equivalent to the one of females and males in phonotaxis (i.e. response, no response). If a male called more during the presentation of the stimulus than during the silent intervals before and after it, his behaviour was scored as a response (Bernal *et al.* 2007). A no response was scored when the baseline calling (during silence) was equal or higher than the response to the experimental stimuli. In the case of the experiments with the natural calls, we compared male vocal behaviour in response to the call of one male directly with the response to the call of the other males. A 'preference' for a stimulus was assigned to the call with the highest calling response for each pair of natural calls.

3. RESULTS

Females exposed to white noise, which mimics only the call's temporal pattern, do not respond to the stimulus (exact binomial test, $p=1.0$). Males, by contrast, vocally respond to the whine-like noise, calling more during the presentation of this experimental stimulus than during spontaneous calling (Wilcoxon signed-ranked test, $Z=-2.703$, $p=0.007$). Calling males not only recognize this stimulus but also increase their vocal response significantly more to the whine-like noise than to the conspecific call (Wilcoxon signed-ranked test, $Z=-2.449$, $p=0.014$). Females and males significantly differ in their responses to whine-like noise calls (Fisher's exact probability test, $p<0.0001$).

A parallel pattern emerges in recognition of the calls with altered harmonic composition. The majority of the energy of the whine is distributed into five harmonic frequencies, in which the first harmonic contains approximately 50 per cent of the energy. Using a synthetically generated call, we evaluated how túngara frogs perceive whines without the first harmonic. We examined the responses of both sexes to a call constituted by the average frequency contour of the upper harmonics. While males call back in response to whines missing the first harmonic (comparison against spontaneous calling, Wilcoxon signed-ranked test, $Z=2.793$, $p=0.005$), females do not exhibit phonotaxis to such calls (exact binomial test, $p=1.0$). Thus, as theory predicts, females are more selective than calling males.

Although males of most species of frogs probably use the conspecific mating call as a beacon to locate calling sites, there are few studies of male phonotaxis (Ryan 1985; Bee 2007). We examined males in phonotaxis tests to the same set of stimuli tested for male-evoked calling and female phonotaxis: whine-like noise and altered harmonics. In the context of phonotaxis, the response of males was almost identical to that of females (Fisher's exact probability test, $p=1.0$ on both comparisons; figure 3). Males approaching a conspecific call did not significantly

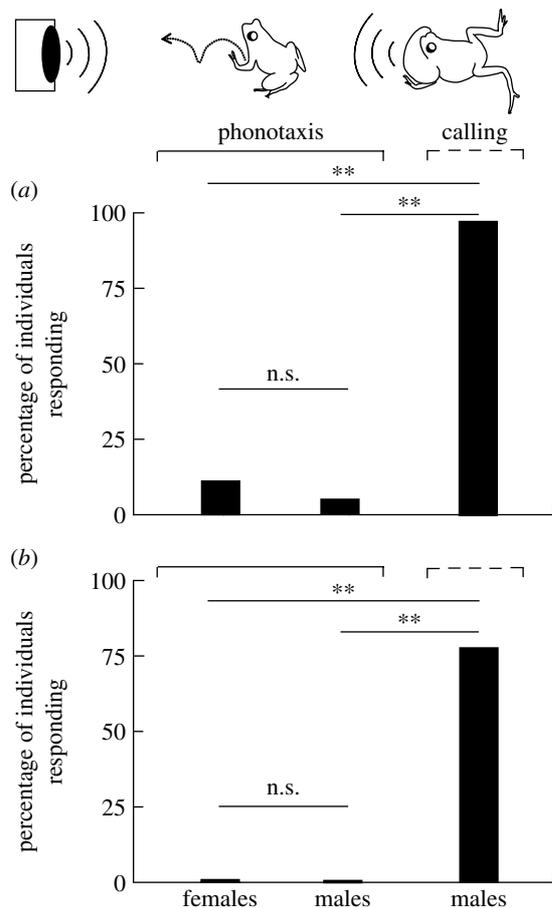


Figure 3. Recognition of advertisement calls with altered frequency characteristics by male and female túngara frogs. The bars indicate the percentage of individuals that responded to the experimental stimulus in each test either by showing positive phonotaxis or an increased vocal response. (a) Responses to 'whine-like noise'. (b) Responses to whines with only upper harmonics. In both sets of experiments, females and males performing phonotaxis agree in their responses (n.s., Fisher's exact probability test, $p=1$ for all comparisons), but not with the ones of calling males (Fisher's exact probability test, $**p<0.0001$ for all comparisons).

respond to whine-like noise or calls with the upper harmonics only (exact binomial test, $p=1.0$ for both experimental stimuli). Therefore, there is no difference between the responses of females and males when we contrast the sexes performing the same behaviour. The responses of males and females in phonotaxis, however, are discordant in the responses of calling males to the same calls (Fisher's exact probability test, $p<0.0001$ for both comparisons).

To further determine whether task influences signal permissiveness, we examined more subtle signal variation encountered in the wild. We evaluated the response of males and females to natural calls. The calls of two males (A and B) elicited similar responses in both sexes and both tasks; those two natural calls elicited more calling by males and preferential phonotaxis by males and females compared with the synthetic call (figure 4*a,b*). In response to the calls of males C and D, however, there were consistent differences based on task, but not sex, that mirrored the differences shown in the experiments with synthetic calls (figure 4*c,d*). Males called more to these two natural calls compared with the synthetic call, while

both males and females preferred the synthetic call (of male C) or showed no phonotactic preferences (call of male D). Again, both sexes were more selective in phonotaxis than were males in evoked calling.

4. DISCUSSION

We used six sets of sexual signals to examine selectivity in response of males and females. We independently tested selectivity in female phonotaxis, male calling and male phonotaxis in each of these tests. Male calling was significantly less selective than female phonotaxis in response to four of the six stimuli (whine-like noise, upper harmonics only, call of male C and call of male D); the two other stimuli (call of male A and call of male B) were quite attractive to both sexes. In no cases were females less selective than males, and in no case were males in phonotaxis less selective than they were in evoked calling. Thus, when the sexes differed in their responses, females in phonotaxis were always more permissive than calling males. This sex difference, however, was exclusive to males and females performing different tasks. The selectivity of males and females in phonotaxis was statistically indistinguishable when measured with all six stimuli. These data reject the hypothesis that differences in signal permissiveness between calling males and searching females are due to sex (independent of behavioural task) and support the hypothesis that the differences are due to the specific behavioural task typically performed by each sex (independent of sex).

There is no question that across many taxa, including our own (Haselton & Buss 2000), the sexes are different. These differences include behaviour, and sex differences in reproductive behaviour have been a cornerstone of behavioural evolution. But the reproductive tasks of males and females often differ, and sex differences have often been interpreted from males and females performing different behaviours. Our study shows that apparent differences between the sexes emerge from differences in the behaviours themselves and are not intrinsic to each sex. The differences are probably explained by the costs and benefits associated with the behaviours performed, i.e. responding or not responding to the signals. For male and female túngara frogs, the costs of approaching an incorrect signal are higher than those entailed by calling males making the same mistake. Misidentification of a call by a phonotaxing female could result in her mating with a heterospecific male, thus wasting her considerable reproductive investment in eggs. Misidentification by a phonotaxing male could result in him chorusing with only heterospecific males, and such choruses would be unlikely to attract conspecific females. Misidentification when a male is deciding whether to vocally respond to a nearby male seems likely to be less costly than a male making the same misidentification error when joining a chorus. Although we have confidence that the cost for a female in misidentifying a mate should be high, our guess of the relative costs of misidentification of phonotaxing and calling males is speculation.

Males and females in phonotaxis perform the same task, but the consummatory behaviour is different; males ultimately find a calling site while females find a mate. Why do females and males make the same decisions if their ultimate goal is different? Constraints due to reliance on

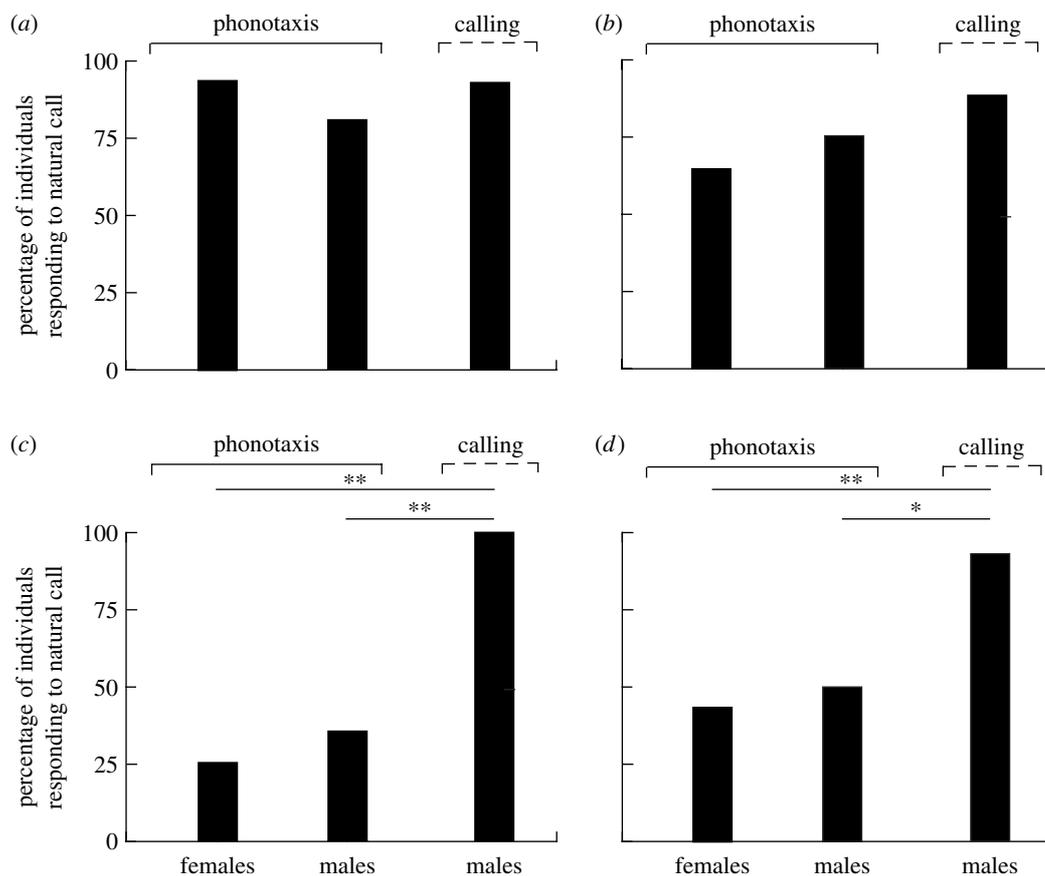


Figure 4. Discrimination of synthetic and natural versions of the advertisement call by male and female túngara frogs. The bars indicate the percentage of individuals that responded to the natural calls in each test either by showing positive phonotaxis or an increased vocal response. (a,b) The responses of both sexes to the calls of males A and B, respectively, independent of task performed, are not statistically different (Fisher's exact probability test, $p > 0.203$ for all comparisons). (c,d) In response to the calls of males C and D, respectively, there are no between-sex differences in phonotactic responses (Fisher's exact probability test, $p > 0.731$ for all comparisons). But the phonotactic responses of both sexes are different from the ones of calling males (Fisher's exact probability test, call of male C: phonotaxis females versus calling males $**p < 0.001$, phonotaxis males versus calling males $**p = 0.001$; call of male D: phonotaxis females versus calling males $**p = 0.017$, phonotaxis males versus calling males $*p = 0.04$).

shared neural systems could drive such commonality between the sexes. Thus, narrow selectivity in responses to sexual signals in male phonotaxis could arise from strong selection acting on female mate choice. Direct selection on each sex could also maintain such similarities. Selective phonotaxis increases the chance of successfully locating a breeding site that is advantageous for both sexes. Another adaptive reason for the sexes coinciding in their stimulus preference and selectivity may rely on males enjoying a benefit for 'mimicking' the behaviour of females. In addition to correctly identifying and joining a chorus of conspecifics, male túngara frogs probably gain a mating advantage by approaching areas where calls preferred by females are broadcast. Consistent with this hypothesis, male spadefoot toads (*Spea multiplicata*) perform selective phonotaxis associating preferentially with conspecific male calls using the same call trait attended to by females (Pfenning *et al.* 2000). In spadefoot toads (Pfenning *et al.* 2000) and túngara frogs (this study), the outcome of any decision-making circuit involved in male and female phonotaxis is similar, although the details of the neural circuitry might differ.

The differences between the sexes in their stimulus selectivity might be due to behaviour-specific responses associated with different effector circuits in the brain, as has been recently suggested of mice (Kimchi *et al.* 2007).

Effector circuits for both broad and narrow selectivity to sexual signals may be present in both sexes. Our results suggest that neural effector circuits for 'female-like' narrow selectivity in response to sexual signals are also present in males. In fact, Hoke *et al.* (2008) showed that in túngara frogs differences between the sexes in stimulus selectivity are the result of differential gating rather than sex differences in the peripheral auditory systems; that is, auditory processing at early stages in the central nervous system is the same in males and females. While activation at lower stages of auditory processing is similar in female and male túngara frogs, the laminar nucleus of the torus semicircularis differentially relays information to motor centres. The results of our study, in conjunction with those of Hoke *et al.* (2008), suggest that, in addition to having a mid-brain gatekeeper, depending on the behavioural output performed, females and males may differ in how such a gatekeeper relays information to forebrain effector centres.

Our study shows that sexual differences in stimulus selectivity are determined by the behaviours performed instead of the sex performing them. In this view, theoretical arguments regarding selection for reproductive strategies still hold, but are applicable to the behaviours expressed rather than to the sex of the individual expressing them. In some species, flexibility in such

expression might overshadow the differences between the sexes (Crews & Fitzgerald 1980; Aubin-Horth *et al.* 2007). In examining the nature of the sexes, behavioural similarities and differences between males and females are central to both the mechanisms understanding common neural pathways and the evolution of behavioural strategies. Future studies should consider the behavioural plasticity of sex as well as its stereotypy (e.g. Crews 1988).

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