



## Wood frogs (*Lithobates sylvaticus*) use water surface waves in their reproductive behaviour

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### Abstract

The ability to sense water surface waves has been described in only a few species, but across a wide taxonomic range. Water surface waves are typically used to localize prey or to avoid predators, and in some cases also for sexual communication. Here we add to the sparse knowledge of the use of this sensory modality by reporting observational and experimental evidence that wood frogs (*Lithobates sylvaticus*) respond to water surface waves generated by conspecifics; that there are pronounced differences in response between males and females; and that they use surface waves in a behavioural context not previously reported for anuran reproductive behaviour: sexual eavesdropping. Because the water waves that elicit the described responses are incidental by-products of calling and locomotion behaviour, we consider this an example of sexual eavesdropping rather than sexual communication. Males quickly and accurately approach a surface wave source, thus aiding in mate acquisition which in this species is mainly achieved by scramble competition. By contrast, females move away from a surface wave source. This may help them avoid sexual harassment by mate-searching males. Because it assures that only the fastest, strongest, and potentially fittest males can amplex them, it may also be a strategy for indirect mate choice by females.

### Keywords

scramble competition, communication, mate choice.

## 1. Introduction

Any object touching or moving at the surface of a water body generates surface waves (sometimes referred to as ripples), and organisms capable of detecting water surface waves can use this environmental cue to sense and localize objects. The ability to analyze water surface waves is found in a few species of a wide range of aquatic organisms, including, frogs,

fish, spiders, insects, and leeches (Schwartz, 1971; Wilcox, 1979, 1995; Lang, 1980; Young et al., 1981; Bleckmann & Barth, 1984; Elepfandt, 1984; Walkowiak & Münz, 1985; Kraus, 1989; Seidel et al., 2001; Harley et al., 2011). Species that detect water surface waves typically use them to localize prey (e.g., Lang, 1980; Bleckmann & Barth, 1984; Schwarz et al., 2011). Fewer species use water surface waves in other behavioural contexts such as predator avoidance (Markl & Hauff, 1973; Vulinec & Miller, 1989) or sexual communication (Wilcox, 1979; Walkowiak & Münz, 1985; Bleckmann & Bender, 1987; Kraus, 1989; Seidel, 1999). The best documented case of the use of this signal modality for communication comes from water striders, which use it in a wide array of contexts including pre- and post-copulatory courtship, sex recognition, repellence of rivals, attractions of females, mate guarding, induction of oviposition, spacing, territoriality and food defence (summarized in Wilcox, 1995).

Perception of water movement plays a critical role in swimming, foraging, and anti-predator responses in amphibian larvae, and also during courtship in some salamanders and newts (Halliday, 1977; Fritzsche & Neary, 1998; Park et al., 2008). The importance of water surface waves in the behavioural ecology of anuran amphibians (frogs and toads) on the other hand, is not well understood, and surface wave sensitivity has only been described/tested in very few species. Among adult anurans, surface wave sensitivity is present in some pipid frogs (*Xenopus* sp., *Pipa carvalhoi*), a largely aquatic ranid (*Rana cyclophlyctis*) and fire-bellied toads (genus *Bombina*) (Elepfandt, 1988). While African Clawed frogs (*Xenopus*) attend to surface waves probably in a prey-seeking context (Elepfandt, 1984), to our knowledge, only fire-bellied toads use surface waves for conspecific communication. Male fire-bellied toads establish territories on the water surface of small ponds and demarcate these territories by surface waves that are produced partly by calling movements and partly by vigorously kicking their hind legs, thus creating concentrically spreading circles on the water surface that are sensed by neighbouring males (Walkowiak & Münz, 1985; Seidel, 1999). Surface wave communication in these species seems to be involved exclusively in male–male competition, and the behaviour of female fire-bellied toads in response to surface waves has not been described (Walkowiak & Münz, 1985; Seidel, 1999; Seidel et al., 2001).

Here we extend the knowledge of the use of water surface waves by animals by reporting that wood frogs (*Lythobates sylvaticus*) respond to water

surface waves, and that they use surface waves generated by calling and locomotion movements of conspecifics in a novel behavioural context: sexual eavesdropping. Several aspects of their behavioural ecology and mating system make wood frogs particularly good study subjects to investigate questions dealing with the use of water surface waves. Wood frogs are explosive breeders (Wells, 2007) which gather in dense aggregations and whose mating activity is limited to one or a few days each year (Howard, 1980; Berven, 1981; Howard & Kluge, 1985). At the breeding pond, males float with outstretched legs on the water surface, calling and swimming around at frequent intervals (Banta, 1914; Berven, 1981). Females mostly remain at the bottom of the pond or clinging to debris beneath the surface, and come to the surface only occasionally (Banta, 1914). Most pairs are formed by males actively searching and clasping females, or struggling with other males for control of females (Berven, 1981). Intense competition can result in several males clasping a single female, leading to the formation of ‘mating balls’, which can result in the death of females by injury or drowning (Howard, 1980; Philips & Wade, 1990; Trauth et al., 2000).

We tested the hypothesis that wood frogs respond to water surface waves and use them in their reproductive behaviour. However, in light of the mating system of this species, which is characterized by explosive breeding, high density, and scramble competition for mates, we hypothesized that males and females would respond differently to water wave stimuli. For males, we predicted that they would quickly and accurately approach the surface wave source, because this would facilitate mate searching. For females, we predicted that they would move away from the wave source because it would decrease the risk of sexual harassment.

## **2. Material and methods**

### *2.1. Behavioural observations*

Behavioural observation took place in a dense population of wood frogs (500+ individuals) during the peak of the 2010 breeding season (1–2 April). We observed the behaviour of mate-searching males as well as amplexed females in response to water surface waves created by the movement of conspecifics.

## 2.2. *Wave stimulation experiment*

On 2 April, we conducted an experiment examining responses to surface waves created by mechanical disturbance of the water surface (see below). During trials (8 pm–11:30 pm) water temperatures ranged from 15 to 18°C, and air temperature ranged from 16 to 21°C.

Stimuli were generated by repeatedly dipping a wooden probe (approximately 1 m long and 1 cm in diameter) into the water. The distance between the subject and the source of the wave stimulus was  $25 \pm 5$  cm. Stimulation was applied for 10 s, or until the test subject moved in response to the stimulus. We tried to keep stimulus rate and amplitude similar between trials by using the same probe moved by the same experimenter (RCK). To obtain an estimate of the rate and consistency of stimulus presentation we analyzed video footage of 25 trials, dividing the duration of stimulus presentation (in s) by the number of presented stimuli. The average stimulus rate was 4.4 Hz (range 3.2–6.4 Hz).

All subjects were approached to within 1.5 m and observed for 30 s in an effort to control for water surface waves created by the movements of the observer and to check for the presence of neighbouring individuals that might affect the trials. (If neighbouring males were present or moved towards the focal male, we aborted the test/observation.) Frogs were randomly assigned to become either a control (observation of movement pattern without stimulation) or an experimental (surface wave stimulation) subject. For control males ( $N = 34$ ), we observed their movement pattern in the absence of stimulation and noted the direction of each movement between calling bouts. If the subject moved in the direction he was facing, we scored the movement as 0°. Right turns were scored as the respective angle between 1 and 180° (to the nearest 10°), and left turns were scored as the respective angle between 360 and 180°. In addition, we noted whether the subject remained floating on the water surface, or dove towards the bottom of the pond. For experimental males ( $N = 60$ ), half of them had the stimulus presented on the right hand side of their body, half on the left hand side (i.e., the direction in which the frog was facing represents 0°, the right side represents 90° and the left side 270°, respectively). Orientation and diving behaviour was scored as described for control males.

All observations/experiments involving males were conducted at the pond by slowly moving through the chorus. We did not mark already tested males,

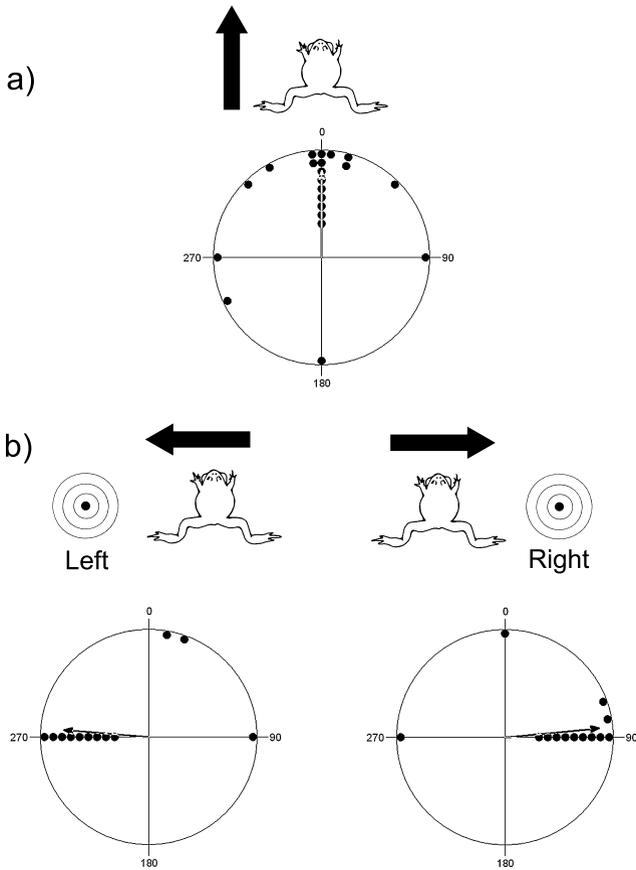
but since males move only short distances at a time, we are confident that by us moving along the shoreline of the pond, we consistently encountered and tested new males.

At the pond, solitary females were quickly clasped by males, or we lost track of females/pairs due to their diving response when surrounded by mate-searching males. Therefore, we conducted experiments involving females/pairs in outdoor tanks (150 × 50 cm, ambient water and air temperature) located ca. 1 km from the pond. We captured pairs ( $N = 4$ ) and transported them to the tanks. We first tested surface-wave responses of females still in amplexus with a male (when in amplexus, it is the female that controls the speed and direction of locomotion; pers. obs.). Then we separated the pairs and re-tested the now solitary females. Stimulation and scoring of orientation and diving responses was performed as described above for experimental males.

For males, we only report one data point per male (each male's first response to the presented wave stimulus). For females, we also present a data set that contains several responses per female, which may include responses as solitary and amplexed female, and in response to stimulation from the left and right side. This inflates sample size, but we opted to include the data because it still serves to illustrate the direction and accuracy of the female response.

### 2.3. *Statistical analysis*

We analyzed the data using circular statistics with the package Oriana v. 3.21 (Kovach Computing Services, Pentraeth, UK). We first tested the null hypothesis that orientation angles were uniformly distributed using Rayleigh tests. If frogs attend to the presented stimuli, orientation angles should not be uniformly distributed, but instead be directed towards or away from the stimulus. We report the angle ( $\mu$ ) and the length ( $r$ ) of the mean vector for each experiment. Since Rayleigh tests indicate only non-uniform distribution but not directionality, we used  $V$ -tests to test for distribution in a specified mean direction. We set expected means for the  $V$ -tests based on visual inspection of the polar diagrams (see Figures 1b, 2). Since males seemed to approach the wave stimuli, we set the expected mean for the male  $V$ -tests at either 90° (towards a stimulus presented from the right) or 270° (towards a stimulus presented from the left). By contrast, females seemed to avoid

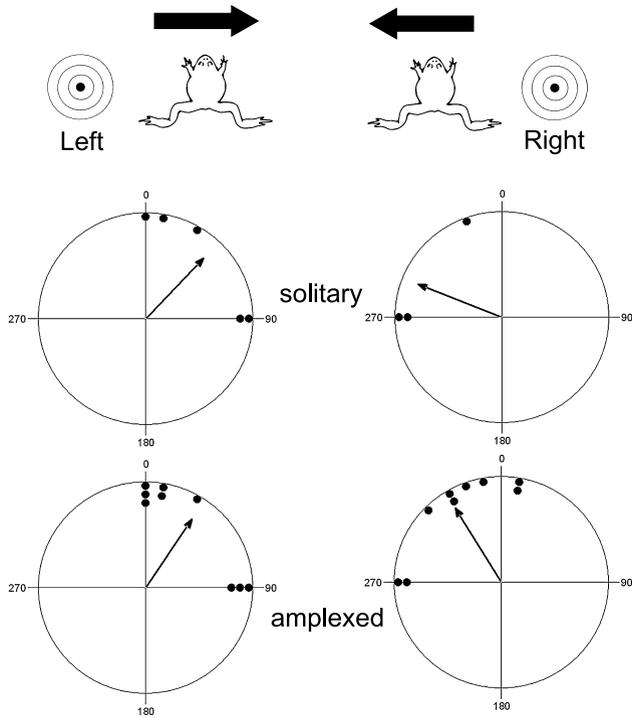


**Figure 1.** Movement patterns of male frogs (main direction indicated by block arrow). a) Control males (not exposed to surface wave stimuli) generally moved straight ahead between calling bouts. b) Males exposed to surface wave stimuli moved towards the source of the stimulus. The circular diagrams show the movement angles of the frogs; the arrow in the diagram denotes the length and direction of the mean vector. Each symbol represents two frogs.

the wave stimuli and we set the expected mean for the female *V*-tests at either  $90^\circ$  (away from stimulus presented from the left) or  $270^\circ$  (away from a stimulus presented from the right).

### 3. Results

Responses of wood frogs to water surface waves typically consisted of a turning component followed by a displacement component, but there was



**Figure 2.** Females (both solitary and amplexed) exposed to surface wave stimuli moved away from the source of the stimulus (main direction indicated by block arrows). The circular diagrams show the movement angles of frogs in response to stimulation from the left or the right; the arrow in the diagram denotes the length and direction of the mean vector. Note that female movement is directed away from the stimulus source, but accuracy is low. Each symbol represents one response.

a pronounced difference between the sexes. Males approached the wave source, while females moved away from it.

### 3.1. Behavioural observations

Male behaviour at the pond consists of call-swim-call-swim behaviour. In the absence of a surface wave, a male generally moved straight ahead (Figure 1a). Upon encountering a surface wave, a male turned and swam towards the source of the surface wave and attempted to clasp it. If the clasped individual was another male he would give a release call, upon which the clasping male quickly released him and resumed the call-swim behaviour. If the clasped individual was a female, the pair entered into amplexus.

Female behaviour was very different. Both solitary females and those already in amplexus moved away when encountering a surface wave and frequently dove to the bottom of the pond, where they remained for extended periods of time. Dives occurred either after a quick turn away from the source of the wave or in the direction females had been facing (which also moved them away from the surface wave source). Males, on the other hand, remained on the water surface, and we never observed a male diving to the bottom of the pond in response to a surface wave.

### 3.2. Wave stimulation experiment

If a male encountered a surface wave stimulus, he turned and swam towards it (Figure 1b, Table 1). Males were very accurate in their turn movements with mean vectors of response 5–6 degrees off from the stimulus source (Figure 1b; Table 1).

By contrast, both solitary females and females in amplexus responded by moving away from the surface wave stimulus (Figure 2, Table 2), showing one of four behaviours: (i) a slow drift away from the stimulus, (ii) a quick turn and swim away from the stimulus, (iii) a quick turn and dive away from the stimulus, or (iv) a quick dive in the direction they had been facing. The accuracy of the turning component of the female taxis movement was comparatively low (mean response vector in females was 22–59 degrees off from a perfect avoidance response; see Figure 2; Table 2).

**Table 1.**

Responses and response accuracy of male wood frogs in response to water surface wave stimulation.

	Stimulation angle	
	Right (90°)	Left (270°)
Sample size	30	30
Mean vector ( $\mu$ )	84°	275°
Length of mean vector ( $r$ )	0.81	0.79
Rayleigh test	$Z = 20.24, p < 0.0001^*$	$Z = 18.51, p < 0.0001^*$
V-test	$V_{90^\circ} = 6.69, p < 0.0001^*$ $V_{270^\circ} = -6.69, p = 1$	$V_{90^\circ} = -6.06, p = 1$ $V_{270^\circ} = 6.06, p < 0.0001^*$

\* Significant difference,  $p < 0.05$ .

**Table 2.**

Responses and response accuracy of female wood frogs in response to water surface wave stimulation.

	Stimulation angle	
	Right (90°)	Left (270°)
<b>Solitary females</b>		
Sample size (females/responses)	3/3	4/5
Mean vector ( $\mu$ )	292°	43°
Length of mean vector ( $r$ )	0.84	0.78
Rayleigh test	$Z = 2.123, p = 0.117$	$Z = 3.06, p = 0.04^*$
V-test	$V_{90^\circ} = -1.91, p = 0.97$ $V_{270^\circ} = 1.91, p = 0.03^*$	$V_{90^\circ} = 1.69, p < 0.05^*$ $V_{270^\circ} = -1.69, p = 0.95$
<b>Amplexed females</b>		
Sample size (females/responses)	4/9	4/9
Mean vector ( $\mu$ )	329°	34°
Length of mean vector ( $r$ )	0.83	0.77
Rayleigh test	$Z = 6.13, p = 0.0007^*$	$Z = 5.43, p = 0.002^*$
V-test	$V_{90^\circ} = -1.83, p = 0.97$ $V_{270^\circ} = 1.83, p = 0.03^*$	$V_{90^\circ} = 1.81, p = 0.04^*$ $V_{270^\circ} = -1.81, p = 0.97$

\* Significant difference,  $p < 0.05$ .

#### 4. Discussion

Wood frogs are among the first anurans breeding in spring, and they are the epitome of an explosive breeder, where mating occurs within only a few nights. This results in high-density assemblages, where most mating opportunities are decided by scramble competition (Howard & Kluge, 1985). For males, a quick and accurate response towards the source of a surface wave is an effective method of seeking out conspecifics and decreasing the cost of mate searching. For females, a response away from the source of a surface wave seems counterintuitive, especially in light of the robust positive phonotaxis shown by females of most anurans (Gerhardt & Huber, 2002). In the context of a scramble competition mating system, however, negative wave taxis is less surprising. First, it may reduce sexual harassment and, thus, decrease mating costs. Although females may gain fitness benefits from enticing competition between males and mating with the presumably fitter contest winner (Cox & LeBoeuf, 1977), for amplexed female wood frogs, approaching additional males carries the risk of becoming the centre of a mating ball, and potentially being drowned or injured by too many males

trying to mate with her (Howard, 1980; Philips & Wade, 1990; Trauth et al., 2000). Second, because it assures that only the fastest, most persistent and potentially fittest male will be able to clasp her, this behaviour could also be a method of indirect mate choice in a mating system that otherwise seems to award females little say in mating decision.

Animals sensitive to water surface waves use this sensory ability in a variety of behavioural contexts. Eavesdropping on predator/prey cues is the taxonomically most widespread use of water surface waves (e.g., Markl & Hauff, 1973; Lang, 1980; Bleckmann & Barth, 1984; Vulinec & Miller, 1989; Schwarz et al., 2011). Communication using water surface waves is less widespread. True communication by surface waves requires not only sensitivity to wave signals, but also specialized behaviour generating such signals, and such behaviour has only been described for some insects, fishing spiders, and fire-bellied toads (Wilcox, 1979; Bleckmann & Bender, 1987; Kraus, 1989; Seidel, 1999). Sexual eavesdropping, where individuals respond to cues that are incidental by-products of calling and locomotion behaviour to negotiate pair formation such as in wood frogs, has to our knowledge not been reported before. Yet, it may be an intermediate step in the evolution of true sexual communication involving water surface waves.

Although taxonomically widespread, sensitivity to water surface waves has been described for only one or a few examples within each taxon (Schwarz, 1971; Wilcox, 1979, 1995; Lang, 1980; Young et al., 1981; Bleckmann & Barth, 1984; Elepfandt, 1984; Walkowiak & Münz, 1985; Kraus, 1989; Seidel et al., 2001; Harley et al., 2011). Several ecological factors should make the use of this sensory modality more likely and may serve to guide further research. First, an aquatic lifestyle is an obvious prerequisite, in particular, for animals that use water surface waves for prey detection and predator avoidance. It is interesting to note that the list of anurans for which surface wave sensitivity has been documented consists of species that have a life-style that is more aquatic than usual for anurans (such as pipid frogs (*Xenopus* sp., *Pipa carvalhoi*), *Rana cyclophlyctis* and fire-bellied toads (*Bombina* sp.; Elepfandt, 1988). Second, the use of surface waves for sexual behaviour (including territoriality, sexual communication, and sexual eavesdropping) may be facilitated by mating systems in which (i) other modes of communication do not play a major role, (ii) the short-distance range of the surface wave modality is sufficient, and (iii) scramble competition

is prevalent. Woods frogs show all of these characteristics: (i) acoustic communication does not seem to play a major role in female mate choice (Bee, pers. com.), (ii) mating aggregations are generally high density which facilitates the effectiveness of short-range cues, and (iii) wood frog males engage in scramble competition (Berven, 1981).

In species with a defined breeding season, behaviour associated with reproduction is frequently temporally limited and not expressed during other periods of the year. For example, male anurans call almost exclusively during the breeding season, which can range from a few nights to several months (Wells, 2007). Phonotaxis, the behaviour during which female frogs approach their mate guided by his mating calls, is temporally even more limited to only a few hours after ovulation (Gerhardt & Huber, 2002; Wells, 2007). Similar temporal limitations may apply for sexual eavesdropping or communication involving water surface waves. In their study on fire-bellied toads, Walkowiak & Münz (1985) could only elicit positive wave taxis in males that also showed spontaneous calling behaviour, i.e., males that were engaged in other integral components of territorial maintenance and reproductive behaviour. In our study on wood frogs, we were able to reliably elicit the described responses to surface waves during the two nights of peak breeding activity, but about a week later at the tail end of the breeding season, when strong chorusing had ceased (yet the remaining males were still calling), attempts to elicit the wave taxis in males failed completely. This suggests that sexual eavesdropping, or communication, involving water surface waves may be more prevalent in anurans than currently appreciated, but difficult to document because it may be only expressed in conjunction with other behaviours such as calling or territorial defence, or temporally limited to the very peak of the breeding season.

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