Frogs flee from the sound of fire

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Fire has an important role in the sensory ecology of many animals. Using acoustic cues to detect approaching fires may give slow-moving animals a head start when fleeing from fires. We report that aestivating juvenile reed frogs (*Hyperolius nitidulus*) respond to playbacks of the sound of fire by fleeing in the direction of protective cover, where they are safe. This is a novel response to fire not known to occur in other animals. Moreover, we identify the rapid rise-time of the crackling sound of fire as the probable cue used. These results suggest that amphibian hearing not only has evolved through sexual selection, but also must be viewed in a broader context.

Keywords: bioacoustics; fire ecology; anurans; *Hyperolius nitidulus*

1. INTRODUCTION

Organisms living in a fire-prone habitat have developed unusual sensory abilities to detect fires. For example, some species of buprestid beetles are attracted to forest fires that they detect with specialized infrared organs and antennal olfactory receptors (Schütz *et al.* 1999; Schmitz *et al.* 2000). Many insectivorous birds are drawn to fire where they catch fleeing insects, while numerous ungulate species concentrate on burnt areas to feed on sprouting grasses (Booyesen & Tainton 1984). Most animals, however, avoid fires by fleeing, or if this is not possible, by burrowing into the substrate or seeking shelter in crevices (Booyesen & Tainton 1984; Geluso *et al.* 1986; Wright 1988; Withgott & Amlaner 1996). Ticks, for example, drop to the ground when sensing smoke and seek shelter (Booyesen & Tainton 1984). No animal has been shown to use acoustic cues, although for slow-moving species this would provide a more long-range detection mechanism than smoke or heat.

The reed frog (*Hyperolius nitidulus*) is a denizen of the West African savannah. During the dry season, juvenile frogs aestivate in an exposed position, typically on dry grass stems or leaves 1–2 m above ground, where they are vulnerable to savannah fires. Whether reed frogs perish or survive fires to recolonize burnt areas remains enigmatic.

By aestivating above ground for several months, frogs are exposed to high levels of solar radiation and high water-vapour pressure deficits. Among the major problems encountered are evaporative water loss, energy constraints and osmotic regulation. Juvenile reed frogs show numerous adaptations that enable them to survive these harsh climatic conditions (Withers *et al.* 1982; Kobelt & Linsenmair 1995; Linsenmair 1997; Schmuck & Linsenmair 1997). While aestivating, frogs adopt a characteristic water-conserving posture, thereby shielding those skin areas that are least waterproof. To maintain waterproofing, vulnerable skin areas need to be protected from dust and dirt. Thus, seeking shelter in cracks in the ground or in underground burrows, where skin would become soiled, is not an option.

In early December 1981, one of us (K.E.L.) observed aestivating juvenile West African *H. nitidulus* in the Comoé National Park, Ivory Coast, fleeing from an approaching fire, and moving from open savannah in the direction of gallery forests and small clumps of trees and bushes on former termite mounds. Such sites, among others, provide protection from fire. Frogs were unlikely to have used visual cues, the smell of smoke, or heat to detect the fire as it was more than 20 m away. The fire had just started and was rather cold due to the fact that the vegetation was not yet completely dried out. This indicates, therefore, that frogs fled in response to the crackling sound of the fire. In the Comoé National Park, fires occur from the end of November until March. Over 80% of the open savannah is burned annually by poachers to attract game to fresh grazing areas (Laugie 1995), by game wardens to improve visibility and, in very rare cases, perhaps also by lightning. In general, fire has been laid in Africa for over 50 000 years (Hopkins 1992; Archibold 1995), indicating that there has been ample time for an evolutionary response to fire by savannah-dwelling reed frogs.

We investigated experimentally whether acoustic cues were sufficient in eliciting the escape response of *H. nitidulus* using playback experiments in the field. We tested the hypothesis that aestivating frogs can hear the sound of fire and respond by fleeing into a nearby fire-resistant habitat where they are safe. In addition, we investigated which spectral and/or temporal characteristics of the sound of fire are likely to be used as cues.

2. MATERIAL AND METHODS

(a) Study area

Field work was conducted in the Guinean savannah region of Comoé National Park, Ivory Coast (8°5'–9°6' N, 3°1'–4°4' W) in January 2001. The tree-scrub-savannah in this region is characterized by distinct dry and rainy seasons. The core dry season lasts from December to February. Most fires occur in the first half of the dry season.

(b) Playback experiments

Juvenile aestivating frogs were located in the field at midday, when they are least likely to be disrupted, and carefully approached to avoid disturbance. After setting up an amplified

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Figure 1. Response of 20 juvenile aestivating reed frogs (*H. nitidulus*) to acoustic playbacks of white noise, reverse fire and fire.

speaker *ca.* 1 m from the frog, we waited 2 min before presenting frogs with the acoustic stimuli. In the first experiment, frogs were offered three stimuli that were broadcast in order of increased likelihood of reaction: (i) with white noise (control 1); (ii) a reversed fire stimulus (a recording of fire played backwards, control 2); and (iii) a fire stimulus (a recording of fire played forward). In a second experiment, only a fire stimulus was presented to control for any other effects that may have influenced the response in the first experiment.

For the first experiment, 20 aestivating frogs were tested during the early dry season. Stimuli were presented with a Sony WM-DC6 tape recorder and broadcast with a Sony SRS-67 amplified speaker mounted on a tripod. The sound of fire had been recorded 1 m from a small savannah fire with a Sennheiser MKE 300 and a Sony WM-DC6 tape recorder. A 2.5 s segment was selected from the recording for the fire stimulus, and a tape loop generated with the program *SOUNDEDIT*. The same segment was reversed and a tape loop created for the reversed fire stimulus. The white noise stimulus was generated with *SOUNDEDIT* and encompassed frequencies from 0 to 10 kHz. The white noise stimulus was presented first, followed by the reversed fire and fire stimulus. The order of presentation was not randomized because we expected frogs to respond most strongly to the fire stimulus by jumping away, thus preventing playbacks of controls. The stimuli were normalized for peak sound pressure level. Each stimulus was presented for 4 min with pauses of less than 1 min between stimuli if frogs did not respond. When frogs moved or jumped from their perch the next stimulus was presented 15 min after frogs had resumed their water conserving posture. Ten frogs were collected the day before and allowed to fully hydrate by placing them in water for 1 h on the day of the experiment. Frogs were then placed on their aestivation site of the previous day at 12.00. All frogs immediately went into the typical water-conserving posture. They were then tested after 1 h. On the same day, 10 other frogs were tested that had not

been handled and thus their hydration state was not known. As the two groups of frogs did not differ in response, the data were pooled.

In a further experiment, we documented the full escape response by continuously playing the sound of fire to individuals until they reached protective fire-resistant sites. As a fire stimulus, we used a new recording of fire that had the same very broad spectral characteristics as the previous recording. It did, however, differ significantly in the average rise-time of tone bursts (mean $\pm$ s.d. of 0.6 ± 0.2 ms; range 0.3–1.0 ms; $n = 20$; t -test: $t = 3.3$, d.f. = 38, $p < 0.01$), an average difference of 0.2 ms. This difference, however, is unlikely to be relevant biologically. At the beginning of the playback experiment, the speaker was mounted on a tripod *ca.* 90° to what was judged to be protective cover by the experimenter, in order to avoid standing in the way of the prospective path taken by frogs. This procedure also helped to rule out that frogs were simply jumping away from the recording (180°). As soon as frogs jumped, the speaker was taken from the tripod and hand held at a distance of *ca.* 1 m from the frog, perpendicular to its direction of movement, and followed until it reached fire-resistant cover and went into a water-conserving posture. Thus, the frogs were continuously presented with the fire stimulus until they stopped fleeing.

(c) Analyses

Acoustic features of the sound of fire and reverse fire were analysed by digitizing recordings at a sampling rate of 22 kHz and 8 bit using *CANARY 1.2* (Bioacoustics Research Program, Cornell Laboratory of Ornithology). Statistical analyses followed Zar (1999).

3. RESULTS

Frogs reacted strongly to the fire stimulus by raising their heads, scanning their surroundings and then jumping onto adjacent vegetation, as a first step towards safety in vegetation that does not burn. The response to the fire stimulus was significantly greater than that expected if frogs reacted randomly to the playbacks (χ^2 -test: $\chi^2 = 21$, d.f. = 2, $p < 0.001$; figure 1). The response was also significantly higher to the fire stimulus than to the reverse-fire stimulus (χ^2 -test: $\chi^2 = 6$, d.f. = 1, $p < 0.05$; figure 1).

To eliminate the possibility that the escape response to the fire stimulus was caused by a sequence effect caused by first presenting both control stimuli, the response of an additional 10 frogs to a fire stimulus only was tested in a second experiment. All 10 frogs responded by jumping from their perch, and moving in an approximately straight line towards what were judged to be fire-resistant habitats, i.e. those not burnt by the typical ground fires: dense bushes, nearby trees or the gallery forest of the Comoé river (table 1). In this experiment, the sound of fire was played to frogs until they reached such fire-resistant sites or were lost in dense vegetation (two cases). The mean $\pm$ s.d. response latency was 160 ± 149 s, suggesting that frogs did not respond to single crackling sounds that might be produced by large birds or mammals walking over dry sticks. Instead, they appeared to integrate over a period of time ranging from 45 to 535 s. The duration of escape, and distance travelled, were likely to be affected, primarily, by the distance to fire-resistant cover. Frogs 3 and 10 (table 1) were lost from sight before they went into a water-conserving posture, indicating that they moved even further.

Table 1. Response of aestivating frogs to the playback of the sound of fire.

frog	response latency (s)	duration of escape (s)	horizontal distance travelled (m)	type of fire-resistant site
1	190	130	1.0	tree (10 m tall)
2	535	252	2.1	small tree (5 m tall)
3	245	120	3.0	dense bush at edge of gallery forest
4	85	465	3.5	tree (10 m tall)
5	180	250	4.4	tree (20 m tall) at edge of gallery
6	170	800	9.3	dense bush at edge of gallery forest
7	150	890	10.8	bush at edge of forest
8	62	526	14.1	dense grass near gallery forest
9	45	655	14.5	tree (15 m tall)
10	105	935	16.6	tree (30 m tall) at edge of forest

Figure 2. Direction of flight response shown by 10 aestivating juvenile reed frogs. The speaker (filled square) broadcasting the sound of fire was placed at *ca.* 90° to what was judged to be protective cover. The arrow shows the mean direction (84°) and strength of the preference ($r = 0.75$).

After escaping horizontally (1.0–16.6 m), frogs moved an additional vertical distance up bushes or trees (0.5–3.8 m). In all but one case, the direction of escape was within 60° of what was thought to be the nearest cover (figure 2). In one case, the frog jumped in the direction of the speaker. The mean angle between speaker and escape direction was 84°, closely matching the direction of fire-resistant sites that was set at *ca.* 90° by the experimental protocol. This escape direction departed significantly from random (Rayleigh test: $w = 5.57$, $r = 0.75$, $p < 0.05$, $n = 10$).

4. DISCUSSION

Reed frogs ignored the control noise stimulus, showed a low response to the reversed sound of fire (6 out of 20) and almost all (18 out of 20) reacted to the sound of fire. The escape response was directed, with frogs mostly moving towards tall trees or dense vegetation near the gallery forest. The strong response of reed frogs to the sound of fire is unlikely to be caused by spectral characteristics, as the reversed-fire stimulus was identical to the fire stimulus in frequency components. The characteristic acoustic feature of these savannah fires is the crackling sound caused

by the rapid rise-time of broad-frequency sound bursts (figure 3*a,c*). These bursts reach a peak amplitude within 0.8 ± 0.3 ms (mean $\pm$ s.d.; range of 0.3–1.2 ms; $n = 20$). Such rapid rise-times are absent in other environmental signals, such as the rustling of dry leaves caused by running lizards (T. U. Grafe, unpublished data), sounds that should not evoke an escape response in reed frogs. Reversing the fire stimulus caused the rise-times of sound bursts to become fall-times, and vice versa. We suggest that the low response to the reverse-fire playback is the result of relatively fast fall-times shown by the sound of the true fire, that become rise-times in the reversed-fire stimulus (mean $\pm$ s.d. of 4.0 ± 1.2 ms; range of 1.7–5.8 ms; $n = 20$). The most probable explanation is that frogs may perceive a proportion of the sound bursts in the reversed-fire stimulus as being short enough to indicate a nearby fire. An additional experiment could present reed frogs with fire sounds with varying rise-times.

It is interesting to note that the advertisement call of *H. nitidulus* also has a fast rise-time (mean $\pm$ s.d. of 1.0 ± 0.2 ms; $n = 10$; T. U. Grafe, unpublished data; figure 3*b,d*), indicating that fast call rise-time may be an important feature in the perceptual landscape of these frogs. At least in one anuran, the grey treefrog (*Hyla versicolor*), rise-time has been shown to affect selective phonotaxis. Females in this species discriminate between pulses in which rise-time differs by only 5 ms: they prefer pulses with a slow rise-time (Gerhardt & Schul 1999). *Hyperolius nitidulus* appeared to be able to detect rise-times of at least 1.2 ms (the maximum rise-time of bursts in the fire stimulus), probably even less. Taking average fall- and rise-times into consideration, many individuals were able to discriminate between rise-times of 4.0 and 0.8 ms, a difference of only 3.2 ms. In *H. versicolor*, rise-time is probably coded by highly phasic neurons found in the dorso-lateral nucleus (Gerhardt & Schul 1999). Sensitivity to rise-time may be a central requirement to detect fire, and distinguish it from other sounds, and such sensitivity may be selected for in anurans that regularly encounter fire.

Further trials were conducted in February and March, however, frogs showed no escape response when presented with playbacks of fire, indicating that there is a time-window in which frogs respond that persists, at least, from mid-December until early January, the period of most frequent fires.

Figure 3. Power spectra (*a,b*) and oscillograms (*c,d*) of the sound of fire (*a,c*) and the advertisement call (*b,d*) of *H. nitidulus*.

It appears that aestivating frogs should always respond to fire. However, an approaching fire may shift its course, according to wind direction and the extent and location of previously burned areas. Apparently, the risk of perishing by fire is weighed against the risk of dying due to desiccation and starvation. Towards the end of the dry season, the latter increases, whereas the former may be reduced because savannah fires occur much less often, thus reducing the selective pressure to escape.

In anurans, auditory perception of airborne sounds is thought to be used primarily during intraspecific communication, and judged to be the result of sexual selection (Fritzsche *et al.* 1988; Ryan 2001). Apart from this study, we know of no other experimental evidence that anurans use airborne sounds other than during intraspecific communication, although this has been investigated. In one study, cane toads (*Bufo marinus*) were observed to prey on tungara frogs, most probably locating them acoustically (Jaeger 1976). Another study investigated experimentally whether female *H. versicolor* avoided calling predatory bullfrogs (*Rana catesbeiana*) while approaching conspecific males, and whether males avoided calling near bullfrogs, but found no effect (Schwartz *et al.* 2000). Several anurans respond to substrate vibrations. The white-lipped frog (*Leptodactylus albilabris*) can use its vocal sac to strike the substrate (Narins 1990). The resulting seismic vibrations may help to attract females or repel males. Spadefoot toads (*Scaphiopus*) are remarkable in being able to detect the substrate vibrations produced by raindrops, enabling them to emerge from underground immediately to make use of temporary ponds for breeding (Dimmitt & Ruibal 1980).

In summary, our experiments demonstrate that juvenile reed frogs can detect the sound of fire, and respond adaptively by escaping towards fire-resistant cover. We suggest that frogs respond to the sharp rise-time of tone bursts that are characteristic of fire. This demonstrates, for the first time to our knowledge, that amphibians detect and respond to airborne sounds in additional, largely unexplored, contexts not just during intraspecific communi-

cation. Future studies on the adaptive significance of auditory tuning and temporal pattern recognition in anurans will have to take this into account. This study indicates that hearing, at least in some anurans, has evolved under more than just sexual selection. Given the unique characteristics of the sound of fire, it seems probable that other animals may use acoustic cues to avoid or locate fires. Indeed, we have preliminary evidence that another reed frog (*Hyperolius nasutus*) that lives in savannah habitats in West Africa also responds to the sound of fire.

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