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Screaming Calls of *Leptodactylus savagei* (Smoky Jungle Frog) Function as an Alarm for Conspecifics

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ABSTRACT.—Neotropical frogs in the family Leptodactylidae frequently emit a loud scream upon being captured by predators, and the leptodactylid scream call was first classified as a distress call functioning to startle would-be predators into releasing prey frogs. Other authors, however, have suggested that scream calls function to warn nearby conspecifics of a predator threat (i.e., an alarm call) and/or to attract larger secondary predators to distract and/or predate the primary predator. In this study, we used a repeated-measures playback experiment to test whether *Leptodactylus savagei* (Smoky Jungle Frog) in Costa Rica responds to scream calls in ways consistent with the call functioning as an alarm. If scream calls emitted by individuals during predation events serve to warn nearby conspecifics of a predator threat, we predicted that scream calls would elicit elevated flight responses compared to when individuals are exposed to advertisement calls or control grey-noise treatments. We observed five primary behavioral responses: individuals flattened their bodies, faced their dens, fled into the dens, faced the audio treatment, and called back with a territorial vocalization. Behavioral responses differed by treatment: scream calls elicited a greater proportion of flight responses whereas advertisement calls caused individuals to demonstrate more interest in the call (particularly females). Our results suggest that *L. savagei* respond to screaming calls from conspecifics by fleeing in ways consistent with the call functioning as an alarm. Future studies are needed to test whether scream calls also function as a distress call and/or to attract secondary predators.

Frogs use a diverse repertoire of vocalizations to interact with conspecifics and heterospecifics and to promote fitness. The diversity of frog calls was recently classified into three major categories: reproductive calls to facilitate breeding between the sexes, aggressive calls to facilitate territorial interactions among individuals, and defensive calls to prevent predation (Toledo et al., 2014). More specifically, among defensive calls, three different types have been described: alarm, distress, and warning calls. Alarm calls are vocalizations made when individuals detect an approaching predator and flee (usually with a single note). Distress calls are a single note or series of loud call notes made when an individual is attacked; the calls are an attempt to shock the predator into releasing the individual (Bogert, 1960). Last, warning calls alert a potential predator that the individual is dangerous before the predation attempt occurs. While this classification system provides a template for defining and understanding the diversity of anuran vocalization phenotypes, classification of calls can be complex, difficult to ascertain, and may fit into more than one category, and experiments are needed to resolve the function and classification of calls (Toledo et al., 2014).

In the New World tropics, frog species in the family Leptodactylidae are known to exhibit a repeated loud and shrill scream call upon being captured by predators (including humans), a vocalization which has been primarily classified as a distress call (Scott and Limerick, 1983). Hödl and Gollmann (1986) reviewed information about leptodactylid scream calls and provided three hypotheses for the functional significance of those calls. First, the authors suggested that scream calls are primarily used as a distress call to startle predators and give individuals a chance to escape (distress call hypothesis; as in Scott and Limerick, 1983). A few observations about the nature of the calls, however, suggest an additional and perhaps more complicated function(s). While Hödl and Gollmann (1986)

found that 60% of *Leptodactylus savagei* emitted distress calls when handled, they also observed that screaming individuals did not physically struggle when attacked. Because the frogs do not actively try to escape while screaming, and scream calls are repeated rather than being emitted in brief and explosive bursts (Högstedt, 1983), these observations suggest that screams might not serve to facilitate escape but rather act as a signal to other individuals. Therefore, a second hypothesis is that scream calls may also function in part to warn kin or other conspecifics as an altruistic alarm call (alarm call hypothesis; Högstedt, 1983; Hödl and Gollmann, 1986). Additionally, the scream calls sound outwardly similar to the calls emitted by juvenile caiman (*Caiman crocodylus*; Scott and Limerick, 1983), a sympatric crocodylian species in frog breeding habitat with parental care where hatchling caiman call to their mothers to solicit protection in response to perceived predation threats. Because the leptodactylid scream calls sound similar to juvenile *C. crocodylus* calls, and natural history observations suggest that *C. crocodylus* may be attracted to scream calls from leptodactylid frogs (Scott and Limerick, 1983), a third hypothesis is that scream calls function to attract larger, secondary predators, such as *C. crocodylus*, to distract or attack the primary predator attacking the distressed frog (secondary predator hypothesis; Högstedt, 1983; Scott and Limerick, 1983; Hödl and Gollmann, 1986). In this last scenario, frogs may use scream calls as a risky, last-ditch gamble to attract other predators in ways similar to how screaming calls of birds attract larger avian predators (Högstedt, 1983).

In Central and South America, *Leptodactylus savagei* (Smoky Jungle Frog) is a large, territorial frog with high site fidelity in terrestrial burrows from which they forage for food during the nonbreeding season. During the breeding season, males move to temporary wetlands where they advertise for females with a loud series of “whoop” calls (Blankenship, 1993; Heyer et al., 2008). When attacked by predators, however, individuals in some populations emit a loud series of scream calls (Scott and Limerick, 1983), similar to other species in the family Lep-

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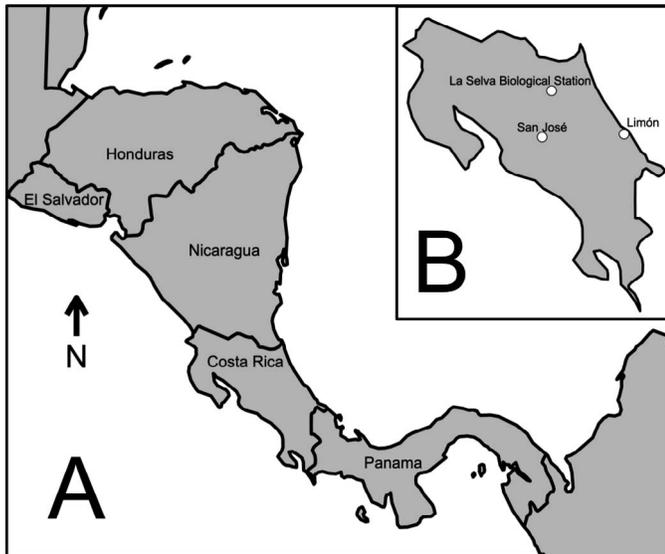


FIG. 1. This study was performed at La Selva Biological Station, a private research reserve in lowland wet tropical forests on the Caribbean slope of Costa Rica. (A) Map of political boundaries in lower Central America including Costa Rica; (B) map of Costa Rica including major cities and the study site.

todactylidae (Hödl and Gollmann, 1986). In this study, we sought to better understand the functional importance of leptodactylid scream calls by performing a repeated-measures playback experiment with *L. savagei*. Specifically, we sought to test the alarm-call hypothesis from Hödl and Gollmann (1986) that scream calls function as an alarm to warn conspecifics of predator threats. If screams emitted by individuals during predation events also serve to warn nearby conspecifics of predation risk, we predicted that individuals subjected to conspecific scream calls would show elevated flight responses compared to when exposed to advertisement calls or grey-noise control treatments.

MATERIALS AND METHODS

During 26–30 November 2017, we performed nocturnal visual encounter surveys to locate *L. savagei* individuals in upland habitats at La Selva Biological Station, Costa Rica (Fig. 1). We marked the location of individuals with flagging tape and then repeatedly visited individuals on consecutive nights to perform a playback experiment. During each visit, we subjected individuals to one of three randomly selected treatments: 1) an audio recording of a typical conspecific scream call, 2) a recording of a conspecific advertisement calls (one individual calling in the typical “whooping” pattern), or 3) a grey-noise (control) treatment. To experimentally simulate acoustic cues, we used a Bluetooth speaker connected to an iPhone 5s to project auditory cues. We placed the speaker between a 45–90° angle perpendicular to the frog and between 30–60 cm away, such that each individual received between 60–70 db of sound. The treatments were then played continuously for 60 sec during each trial during which we recorded behavioral responses exhibited by individuals. When possible, we attempted to survey each individual three times to expose them to each treatment group in a repeated-measures design.

We observed five distinct behavioral responses from individuals during playback trials which we interpreted as suggestive of either defensive flight responses, interest responses, or

territorial responses to acoustic treatments. We categorized defensive flight responses as behaviors where individuals reduced their conspicuousness and exposure to potential predators in the landscape by 1) flattening their bodies to the ground, 2) turning their bodies to face the entrance to their den, and/or 3) fleeing into their den. Conversely, some individuals shifted their body position to face the acoustic cue directly without diminishing their presence above ground 4), which we categorized as an interest response. Last, we observed one adult male who, when prompted with an advertisement call, faced the speaker and emitted four short, low, single-note calls back toward the acoustic cue 5); this call appears to have been an undescribed territorial call that we categorized as a territorial response.

We first analyzed the data using nonparametric Fisher’s exact tests. We performed a Fisher’s exact test to test for differences observed among all individuals across the three treatment groups, and then we performed a pairwise Fisher’s exact test for differences between the advertisement-call and scream-call treatment groups. We used Fisher’s exact test rather than the more conventional Pearson’s chi-square (χ^2) test because sample sizes were small for some behavioral responses. To test the prediction that scream calls drive flight response in *L. savagei* more directly, we then analyzed the data with a generalized linear mixed-effect models (GLMMs). We modeled flight response as a consequence of treatment group and sex using a binomial distribution. Frog identity was set as a random effect to account for repeated measures of individuals. We did not evaluate models with interactions between treatment and sex because our dataset was relatively small and we did not want to risk over-parameterizing the analysis. All analyses were performed in the statistical program R (R Core Team, 2016) with $\alpha = 0.05$. The GLMMs were fitted with the function *glmer* in the package ‘lme4’ (Bates et al., 2015). The audio files used in the experiment and our raw data are available from the figshare digital repository: DOI:10.6084/m9.figshare.7568972.

RESULTS

We assessed the behavioral responses of 35 individual *L. savagei* (females: $n = 27$; males: $n = 8$) with 87 trials. Among all individuals, 60% of individuals were detected on at least three nights and received all three treatments while 20% each were detected on only one or two nights. Females had a higher probability of being present and available for treatment on three consecutive nights (66%) than did males (50%).

We found significant differences in *L. savagei* responses among conspecific scream calls, advertisement calls, and grey-noise control treatments (Fisher’s exact test: $P < 0.001$). We observed a greater proportion of flight responses by individuals when exposed to conspecific scream calls relative to when exposed to advertisement calls or grey-noise controls (Fig. 2). Of individuals that responded to the conspecific scream call, all individuals exhibited a defensive escape response by flattening, facing their den, or fleeing into the den. Conversely, individuals exposed to advertisement calls exhibited more-varied responses including receptive individuals that faced the speaker, a male that called back at the speaker, and individuals exhibiting defensive responses (flattening, facing the den). No individuals responded to grey-noise treatments. Pairwise comparison between conspecific scream call and advertisement call treatments indicated a significant difference in behavioral responses between groups (Fisher’s exact test: $P = 0.011$), where

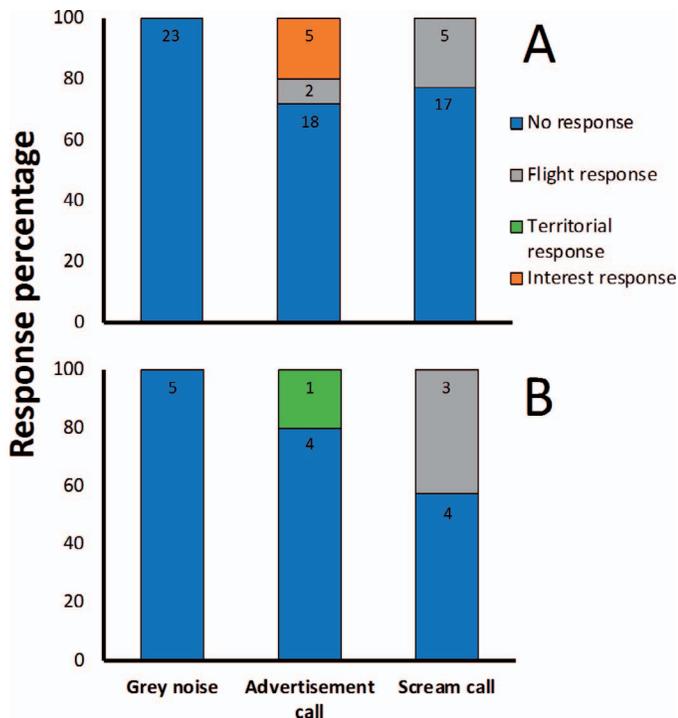


FIG. 2. Behavioral responses of female (A) and male (B) *Leptodactylus savagei* (Smoky Jungle Frogs) in response to simulated conspecific advertisement calls, conspecific scream calls, and control grey-noise treatments at La Selva Biological Station, Costa Rica. The y-axis is scaled by the percentage of observations; the raw number of observations is included within each histogram box.

individuals were 3.6 times more likely to exhibit a defensive flight response when exposed to scream calls relative to advertisement calls (GLMM: $P = 0.046$). Likelihood of flight response did not vary by sex (GLMM: $P = 0.40$).

DISCUSSION

Our field experiment found that *L. savagei* responded to conspecific scream calls with an elevated flight response compared to when individuals were exposed to advertisement calls and a biologically insignificant control. These results were consistent with predictions of the alarm call hypothesis that scream calls act as a cue for conspecific individuals to initiate flight from predation risk. While previous authors have described the screaming calls of leptodactylid frogs as a well-known example of a distress call (Scott and Limerick, 1983; Hödl and Gollmann, 1986; Savage, 2002), our data provide the first experimental evidence supporting a functional importance of scream calls for leptodactylids. Specifically, we suggest that the screaming calls of leptodactylid functions as an alarm call (*sensu* Toledo et al., 2014).

Most alarm calls described for anurans are vocalizations made by individuals where they detect a predator, initiate flight, and call out to warn conspecifics of predation risk while fleeing themselves (Toledo et al., 2014). However, alarm calls during predation have been observed by at least one species, *Phrynohyas venulosa*, when being preyed upon by a snake (Leary and Razafindratsita, 1998); they may represent a call with similar function as that of *L. savagei*. Alarm call behaviors may evolve through cooperation: if individuals use alarm calls to warn nearby related individuals of predation threat and potentially increase the survival and inclusive fitness of

conspecifics, then alarm calls may be altruistic (Trivers, 1971). Alternatively, alarm calls may function whereby callers increase their individual fitness by manipulating conspecifics (Charnov and Krebs, 1975). Opportunity for conspecific manipulation seems unlikely for leptodactylid frogs, however, because leptodactylid scream calls occur only when individuals are under strong and direct attack, and screamers largely lack opportunity to leverage knowledge of the predator relative to conspecifics. This mechanism may be relevant for other anurans that are clustered in space with conspecifics and use alarm calls while fleeing among other conspecifics (e.g., *Lithobates catesbeianus*; Cooper, 2011).

A limitation of our study is that the sample size ($N = 35$ individuals) was relatively small, particularly for males ($n = 8$). While the small number of male observations limits our ability to test for intersexual differences in behavioral responses to auditory cues (e.g., testing for territorial responses to advertisement calls by males), we did observe relatively strong effects within females (the sex with a considerably greater sample size; $n = 27$), and effect sizes of behavioral responses to scream calls (Fig. 2) were generally consistent between the sexes. We may have observed a female-biased sex ratio for many reasons. For one, populations may be naturally female-biased; however, no population demographic studies describing sex ratios have been performed on *L. savagei*, and female-biased sex ratios are uncommon for anurans (Alho et al., 2008). Alternatively, our sample may have been female-biased because females are more detectable and/or more likely to occupy upland habitat at the end of the breeding season than are males. Both factors may have applied in our study, because 1) we found females more likely to be available for experimental treatment on consecutive nights than males, and 2) we performed the study in the wet season, when male *L. savagei* may spend more time occupying lowland aquatic habitats to advertise for mates and may thus be less available in upland habitats than females. A detailed demographic study using mark-recapture methods (e.g., Gibbons, 1990) may be needed to understand patterns of population demography and seasonal habitat use for *L. savagei* while accounting for imperfect detection (Mazerolle et al., 2007).

In conclusion, our results provide experimental evidence supporting functional significance of screaming calls for leptodactylid frogs in which the calls are altruistic alarms for conspecifics; however, we do not rule out the possibility that leptodactylid scream calls may have more than one function. Specifically, future experimental studies are needed to test whether leptodactylid scream calls also function 1) as a distress call to startle predators, and/or 2) to attract secondary predators (Scott and Limerick, 1983; Hödl and Gollmann, 1986). Both the distress call and secondary predator hypotheses would confer functional importance to leptodactylid scream calls, where fitness increases are given to the caller, and neither of these two hypotheses are excluded by our support for the alarm call hypothesis. Future experiments should test for additional functional uses of leptodactylid scream calls and increase our understanding of the complex functions and fitness consequences of defensive anuran vocalizations.

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