

GECKO PHONOTAXIS TO CRICKET CALLING SONG: A CASE OF SATELLITE PREDATION

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Abstract. Insectivorous Mediterranean house geckos, *Hemidactylus tursicus*, are found in the field close to the burrows of calling male decorated crickets, *Gryllodes supplicans*. In playback experiments where adult geckos were presented with calls of these crickets or calls of frogs as controls, geckos exhibited positive phonotaxis to broadcast cricket calling song. This indicates that geckos orient to and approach male cricket calls, even though the crickets call from burrows where they are protected from the geckos. However, this behaviour enables the geckos to intercept and consume female crickets that also respond phonotactically to the cricket calls. Thus geckos act as 'satellite predators', a situation which may impose sex-biased mortality on female crickets.

Male crickets produce species-specific calling songs that function to attract sexually receptive females (Walker 1957; Alexander & Otte 1967). Potential predators may also use these calls to locate prey. Calling male field crickets, *Gryllus* spp. (Orthoptera: Gryllidae), are parasitized by an acoustically orienting parasitoid, *Euphasiapteryx ochracea* (Diptera: Tachinidae), which kills them within about a week (Cade 1975). Tachinid flies are attracted to the calls of other hosts, including katydids (Orthoptera: Tettigoniidae) (Burk 1982) and mole crickets (Orthoptera: Gryllotalpidae) (Mangold 1978), while the sarcophagid fly *Colcondamyia auditrix* exhibits phonotaxis to its host, calling male cicadas (Homoptera: Cicadidae) (Soper et al. 1976). Additionally, signalling male crickets may be susceptible to vertebrate predators such as domestic cats (Walker 1964), spadefoot toads, *Scaphiopus holbrookii* (Walker 1979) and little blue herons, *Florida coerulea* (Bell 1979). Vertebrate prey are also subject to predation by acoustically orienting predators. Recently, Tuttle & Ryan (1981) showed that the bat *Trachops cirrhosus* acoustically orients to and preys on calling male frogs. Using these calls, the bats are able to discriminate between edible and poisonous frogs, and members of large and small species.

During a field study of the decorated cricket, *Gryllodes supplicans*, insectivorous geckos, *Hemidactylus tursicus* (Sauria: Gekkonidae), were observed sitting motionless within 2 m of the burrows of calling male crickets ($N=4$). On one of these occasions, a gecko intercepted a female *G. supplicans* which appeared to be orienting to the calling male cricket. The female subsequently

escaped down the male's burrow, after which the gecko remained immobile over the burrow for several minutes. Another time, a different calling male was apparently disturbed by the investigator and it moved to a new burrow about 1 m further away from the gecko. Within 1 h the gecko had changed its position such that it was again within 2 m of the singing male cricket. Faeces of 2 geckos collected away from the study site contained cricket and other insect remains. These observations led us to test for gecko phonotaxis experimentally, using broadcast cricket calling song. Our evidence suggests that geckos locate at least some of their prey acoustically.

Methods of Study

Geckos were collected from the open stairwells in McCarty Hall at the University of Florida, Gainesville, Fla. They were kept individually in 3.78-litre glass jars provisioned with water and a cardboard cylinder for shelter. Individuals were tested twice for phonotaxis on each of the two consecutive days following capture, and then released. Several non-experimental geckos were maintained on a *G. supplicans* diet for 6 weeks to confirm its suitability as a food source. No attempt was made to sex captive geckos; however, the snout-vent length for 24 of the 29 lizards used in experimental trials was measured to obtain an indication of age. Large geckos (snout-vent length > 5 cm; presumably adult individuals) had a mean snout-vent length of 5.5 cm (SD = 0.2; range = 5.2–5.9; $N=18$). Small geckos (snout-vent length < 5 cm; presumably juvenile individuals) had a mean snout-vent length of 4.3 cm (SD = 0.4; range = 3.8–4.9; $N=6$).

A circular concrete platform (2.44 m diameter \times 0.08 m height) divided into eight equal sectors served as a testing arena; this was located in a windowless room of about 7×5 m. A raised well (14 cm diameter \times 8 cm height) constructed of heavy-gauge metal screen was placed in the centre of the arena and was used to introduce the geckos into it. A sound stimulus (either control or experimental) was broadcast to a gecko in the arena through the speaker of a Uher 4000 Report L tape recorder placed 2.3 m from the centre of the arena in one of the eight sectors. The sound stimulus intensity was set at 76 dB, as measured with a Bruel & Kjaer impulse precision sound level meter Type 2204 (A scale) held 10 cm in front of the speaker. This was comparable to the sound intensity of calling male *G. supplicans* measured in the field. Observations were made from behind a blind suspended from a wall.

Previously recorded *G. supplicans* calling song served as the experimental sound stimulus. This song is a pure-tone signal consisting of 3-pulse chirps at a dominant carrier frequency of 6.6 kHz (Fig. 1A). The control stimulus was the calling song of the spring peeper, *Hyla crucifer*, which is also a pure-tone signal but at a dominant carrier frequency of 3 kHz (Fig. 1B). (Gecko ears are most sensitive to sound frequencies of between

0.1 and 3 kHz; Marcellini 1977). Recordings were made with the sound level meter fitted with a half-inch microphone (4165). Recordings were analysed with a Nicolet 100 A (Fast Fourier Transform) Mini-Analyzer.

The experiment was run during May and June, 1981. Both species are nocturnal and all trials were conducted during 2000–2400 hours under red-light illumination. Control trials were carried out following the completion of all experimental trials and with different geckos. On any given night the temperature varied no more than 2°C ; temperatures ranged from 29.5 to 33.5°C over the course of the entire experiment. In each trial, the speaker was located opposite to and on the midline of a randomly selected sector. A gecko was placed in the well within its shelter, thus minimizing disturbance to the animal and avoiding physical contact. Playback was initiated after an 8-min habituation period or when the animal climbed to the top of the well. Playback continued for a maximum of 12 min. A trial was not considered valid unless the individual left the arena before the expiration of the playback period. The sector from which the gecko left the arena was recorded for each successful trial.

Results

Captive geckos readily consumed and thrived on crickets. Data from the phonotaxis experiment were analysed using the chi-squared test with Yates' correction for continuity. The number of individuals leaving the arena from the three sectors facing toward the speaker was compared with the number of geckos leaving the arena from the three sectors facing away from the speaker (the two remaining central sectors were designated 'neutral'). Geckos did not exhibit any significant response to playback of the control sound (Fig. 2; $P > 0.1$). However, during playback of cricket calling song about twice as many individuals left towards the speaker than away from it, although this result was not statistically significant (Fig. 3; $0.1 < P < 0.2$). However, when only trials of 'adult' geckos are considered (see Methods), the results are significant (Fig. 4). Adult geckos exhibited a positive response to the playback of *G. supplicans* calling song ($P < 0.02$).

Individuals that left the well during playback of cricket song often proceeded slowly in a series of stops and starts. Individuals repeatedly moved their heads from side to side while stationary. Some geckos that were quiescent during the habituation period of a trial began moving around in the well immediately after playback

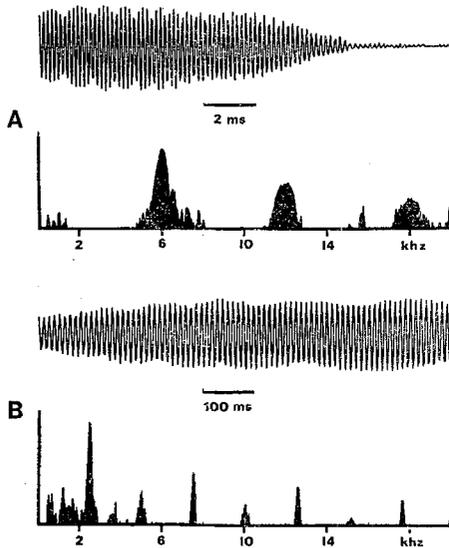


Fig. 1. Oscillogram (upper trace) and frequency spectrogram (lower trace) of (A) *Gryllodes supplicans* cricket calling song and (B) the calling song of the spring peeper, *Hyla crucifer*.

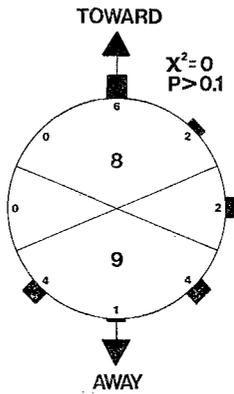


Fig. 2. Response of *Hemidactylus tursicus* geckos to playback of the control sound (calling song of the spring peeper, *Hyla crucifer*).

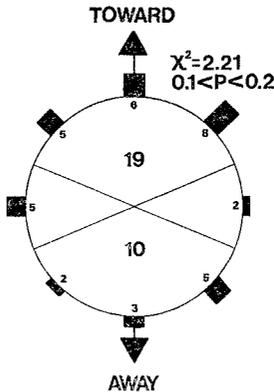


Fig. 3. Responses of *Hemidactylus tursicus* geckos (juveniles included) to playback of *Gryllodes supplicans* calling song.

was initiated. Twice, geckos walked to the tape recorder and remained immobile immediately adjacent to it after leaving the arena. On three other occasions, geckos that left the arena from a sector other than the speaker sector circled towards the tape recorder and remained immobile within 1.5 m of it.

Discussion

Our results demonstrate that adult *H. tursicus* geckos phonotactically respond to the calling song of male *G. supplicans* crickets. The statistical significance of these results is lost when juveniles are included in the analysis. This suggests that juveniles lack the phonotactic response and that this behaviour may be learned.

H. tursicus frequent buildings in Florida, and forage opportunistically near outside lights where insect prey are abundant (personal observations). The situation described here appears analogous: geckos may learn to associate sounds with the acquisition of prey in much the same way they associate lights with prey.

In species such as *G. supplicans* where the parental investment of males is far less than that of females (Alexander 1975), males are expected to assume most of the risks incurred in obtaining mates (Trivers 1972). In most orthopteran mating systems it is the males that are the long-range signallers, and as such they bear the brunt of the predation pressure associated with calling (Burk 1982). Females, on the other hand, normally avoid these risks (Thornhill 1979).

In view of the potential for heavy male-biased predation, an adaptive male strategy is to sing from a concealed space, crevice or burrow which is inaccessible to predators: such is the case with *G. supplicans*. The average width of the entrance to 22 cricket burrows at our site was 6.3 mm (SD = 2.5; range = 2-10), which is too small to allow the passage of a gecko. As expected, the geckos did not attempt to enter the burrows, nor did they try to remove crickets from them. Instead, the geckos sat motionless outside the burrows. Because cricket calling songs attract females, and in some species male conspecifics (Ulagaraj & Walker 1973; Cade 1975, 1979; Campbell & Shipp 1979), this behaviour is potentially adaptive in predators such as geckos. By acoustically orienting to male crickets calling from burrows, geckos are able to intercept and consume phonotactically responding female and

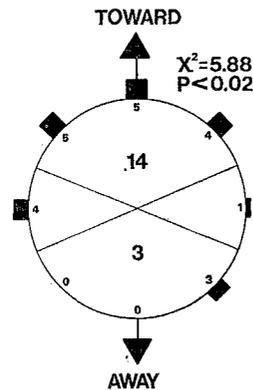


Fig. 4. Responses of *Hemidactylus tursicus* geckos (adults only) to playback of *Gryllodes supplicans* calling song.

male crickets. In the long run, more prey could probably be obtained in this manner than could be if the individual male crickets were eaten.

This behaviour recalls the behaviour of the satellite males described, in a mating context, in some crickets (Cade 1975, 1979) and frogs (Howard 1981). Satellites do not call and thus minimize the potential risks of predation and reduce aggression from other males. Instead, they position themselves near actively calling males and intercept the females responding to callers. Because of the similarities in strategy between the satellite males attempting to mate, and the geckos attempting to feed, we propose the term 'satellite predation' to describe the predatory behaviour of the geckos observed in this study.

A direct consequence of this predatory behaviour is that it is likely to result in female-biased predation in spite of the fact that females do not call. Because they search for and locate males, female *G. supplicans* spend significantly greater amounts of time in the open, outside the safety of burrows than do males, and also move more (Sakaluk, unpublished data). Consequently the females are more exposed to predation, especially since predators are attracted to the precise locations where females are likely to be.

Burk (1982) summarizes the importance of predation on sexually signalling males. It is an important mortality factor. In this study we show that female crickets, although they do not call, also face potential predation simply by responding to signalling males. The implications of this selection pressure for the evolution of mating behaviour of female *G. supplicans* are great, both in terms of anti-predator defences and in the choice of calling males, but the effects of such selection are unknown.

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