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Chemical communication in an archaic anuran amphibian

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Bioacoustic signals appear to be so essential to the social communication of anuran amphibians that other sensory modalities have been largely ignored. We studied the abilities of *Leiopelma hamiltoni*, a species evolutionarily basal to most living anurans, to communicate by means of chemosignals. We collected frogs in the field, held them in captivity for 72 h, and then tested their preferences for substrates that they had marked themselves to those marked by conspecifics. Individuals preferred paper towels that they had marked themselves to those marked by frogs collected from other home ranges. Preferences were greater, on average, when the conspecific had been collected farther away. Frogs did not discriminate between their own odor and those of other individuals with which they had shared a home range. Individuals preferred their own odor to a blank unmarked towel but also avoided odors of unfamiliar conspecifics when paired with a blank. The discovery of chemical communication in an archaic anuran offers a window into how frogs may have communicated before mechanisms of bioacoustic signaling evolved. We suggest, however, that chemical signaling may be widespread in anuran amphibians. *Key words:* frogs, individual recognition, Leiopelmatidae, olfaction, pheromones, self-recognition. *[Behav Ecol 15:88–93 (2004)]*

Their conspicuous vocalizations make anuran amphibians model subjects for studies of communication. Yet, the earliest anurans, represented by extant families such as the Leiopelmatidae (Hay et al., 1995), probably never evolved the ability to communicate socially by means of bioacoustic signals (Bogert, 1960). Other species also may refrain from calling, especially if they live in noisy environments, are likely to attract predators, or lack sympatric congeners with which they might hybridize (Ryan, 2001). Perhaps because bioacoustical studies on anurans have so readily elucidated evolutionary processes of reproductive isolation, speciation, and sexual selection (Gerhardt and Huber, 2002; Littlejohn, 1999; Ryan, 1998), the possibility that frogs and toads communicate through other modalities has been largely ignored.

From single-celled protozoa to primates, chemical cues serve as ubiquitous markers of individual, group, kinship, and species identity (Birch, 1974; Colgan, 1983; England et al., 1999; Hölldobler and Carlin, 1987; Stoddart, 1980; Stoka, 1999; Vander Meer et al., 1998; Wilson, 1970). Social recognition based on chemosignals never has been demonstrated in adult frogs or toads, but multiple factors point to it. Larval anurans recognize predators (Gallie et al., 2001; Morin, 1986; Petranka et al., 1987), injured neighbors (Hews, 1988; Kiesecker et al., 1999; Summey and Mathis, 1998), conspecifics (Kiseleva, 1996), and kin (Blaustein and O'Hara, 1982; Mason et al., 1998; Waldman, 1985, 1986) by sensitive chemoreceptors that become further developed after metamorphosis (Spaeti, 1978). Newly metamorphosed frogs and toads continue to make use of these capabilities (Flowers and Graves, 1997; Graves et al., 1993). Amines and peptides secreted by specialized glands (Clarke, 1997; Erspamer, 1994) may function to deter predators (Williams et al., 2002) but also serve a role in communication. Recent work suggests the existence of sex pheromones (Kikuyama et al., 2002; Pearl et al., 2000; Wabnitz et al., 1999, 2000). Many frogs and toads use their chemical senses to orient and navigate quite precisely to environmental odors (Forester and Wisnieski, 1991; Sinsch, 1990). Thus, anurans both generate potential chemosignals and possess the neural circuitry to perceive and process chemical cues.

Some frogs are ecologically similar to salamanders whose refined abilities to communicate chemically (Dawley, 1998) apparently compensate for their acoustical silence. We studied Hamilton's frog, *Leiopelma hamiltoni*, the rarest surviving member of an ancient lineage of anurans that closely resembles early Jurassic frogs (Rocêk, 2000). Although Hamilton's frogs may startle predators with alarm calls, they are not known to vocalize in a social context (Bell, 1978). They lack the external eardrums that are characteristic of modern frogs and have distinctly salamander-like inner ears (Lewis and Lombard, 1988). Although their hearing thus lacks acuity (Wever, 1985), anatomical studies suggest that their vomeronasal and olfactory systems are well developed (Stephenson, 1951, 1955). Similar to salamanders whose chemosensory abilities have been documented, Hamilton's frogs inhabit the forest floor and demonstrate site tenacity to rocks, logs, and litter, under which they find shelter (Newman, 1990). Both salamanders and Hamilton's frogs care for eggs and young (Bell, 1985; Jaeger and Forester, 1993). Abilities to recognize their home range and progeny by chemical cues thus might be favored by natural selection. We tested whether Hamilton's frogs use chemosignals to communicate, as salamanders do.

METHODS

Study species and site

Hamilton's frog, *Leiopelma hamiltoni*, is endemic to Maud and Stephens Islands in the Marlborough Sounds, New Zealand. The species is one of the rarest, most geographically restricted frogs in the world and is strictly protected. Although Bell et al. (1998) classified Maud Island frogs as a new species (which they named *L. pakeka*), strong genetic similarities between populations on the two islands contradict this view (Holyoake et al., 2001). The frogs occupy a 16-ha stand of remnant native

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forest on Maud Island. We conducted our studies there during October 1997, August 1999, and April 2000.

Experimental methods

We collected frogs that we found on or under rocks in their natural forest habitat during the evening. When we found two or more frogs under a rock, we collected all of them. We mapped the frogs' locations and measured the distances between rocks, which ranged from 0–90 m. We then carried the frogs, each in a separate container, to Comalco Lodge, a field station located just a short distance away. There we transferred each frog to a separate clear plastic box (33 × 20 × 8 cm) lined with clean, moist paper towels. Subjects were held for 72 h within these containers, which were stored in a dark area within a quiet room. Subjects were not fed or disturbed during this holding period.

We conducted tests first to determine whether frogs could discriminate between chemosignals that they themselves had deposited on paper towels and those deposited by conspecifics. Subjects were tested in clean clear plastic boxes of the same type and dimensions as those in which they had been housed. A line was drawn in the center of each box, dividing it into two equal sections. On each side of the center line, we placed a paper towel that had been "marked" during the holding period by the test subject itself or by another frog. Obvious detritus and fecal matter were removed from the paper towels before placing the frogs into testing boxes. Frogs and paper towels were handled with disposable plastic gloves to prevent experimenters from imparting odors onto them.

A frog was placed into the center of the box and allowed to acclimate for 5 min. The subject's movements on either side of the center line (as determined by the position of its snout) then were recorded for 30 min. To control for side biases, the box was rotated 180 degrees, the subject was allowed an additional 5 min to acclimate, and its movements were recorded for an additional 30 min. Half of the subjects were tested initially with their own odor on the right, and the others with their own odor on the left. Tests were conducted outside in well-shaded areas during daylight hours. Observers were unaware of the stimuli on each side as they recorded subjects' movements. Although we matched subjects and conspecifics used in each test by size, subjects were not precisely measured until the completion of experimental tests (mean ± SD, snout-vent length = 37.8 ± 5.9 mm). *L. hamiltoni* cannot be reliably sexed by external traits, although adult females tend to be larger than males (Bell, 1995).

Sixty frogs were tested, 20 under each of three conditions corresponding to their opportunities for interaction before the start of the experiment. Subjects were tested for their tendency to discriminate between their own odors and those of conspecifics with which they had been found (under the same rock), between their own odors and those of neighbors found in nearby localities (less than 5 m), or between their own odors and those of unfamiliar frogs collected from distant localities (more than 5 m). Detailed studies of the ecology of *L. hamiltoni* on Maud Island suggest that individuals show strong site fidelity and rarely wander more than 5 m from their home site (Newman, 1990).

Further tests were conducted to determine whether frogs were attracted to their own odors, repelled from conspecifics' odors, or both. Experimental procedures were the same as those described above except with respect to the stimulus choice presented to subjects. In the first series, frogs were given a choice between a paper towel with which they had previously been in contact and an equivalently moistened "blank" paper towel with which no frog had been in contact. In the second series, frogs were given a choice between a paper towel with which a conspecific had been in contact and a moistened blank paper towel. Twenty subjects were tested in each series. For 10 trials of the second series, paper towels had been marked by frogs collected within 5 m from the subject. For the other 10 trials, paper towels had been marked by frogs collected from distant rocks (more than 5 m).

Each subject was tested only once. Plastic testing boxes were thoroughly washed with 95% ethanol and then rinsed with rainwater between tests. At the conclusion of experiments, all frogs were returned to the exact localities from which they had been collected in the forest. We toe-clipped some individuals for further genetic analyses that are currently underway.

Statistical analyses

For each experiment, the amounts of time spent by subjects on either side of the center line were compared. Differences were normally distributed, and thus were analyzed by paired t tests. In addition, numbers of individuals that spent most of their time on each side were compared for each experiment by binomial probabilities. The magnitude of subjects' preference for their own odor to their conspecifics' odor (difference between times spent on each side) was analyzed as a function of the distance between their collection sites by one-way ANOVA. All statistical inferences were based on two-tailed probabilities. Statistical analyses were conducted with Minitab 13.30.

RESULTS

Self/nonself recognition

Most frogs frequently moved around their testing box during the 1-h experimental periods. Of those subjects tested for their preference for their own paper towel versus that of a familiar conspecific, collected under the same rock, 12 spent most of their time on their own side and eight spent most of their time on the conspecific's side (p = .50, binomial probability). Subjects did not spend different amounts of time on their own paper towel versus that of their familiar conspecific (t = 0.07, df = 19, p = .94).

Subjects given a choice between their own paper towel and one marked by a neighbor, collected within 5 m, showed a strong preference for their own odor. Sixteen frogs spent most of their time on their own side, and four spent most of their time on the conspecific's side (p = .012, binomial probability). Subjects spent significantly more time on their own paper towel than on that of their neighbor (t = 2.37, df = 19, p = .028).

Subjects given a choice between their own paper towel and one marked by an unfamiliar conspecific, collected farther than 5 m away, also demonstrated a preference for their own odor. Fifteen frogs spent most of their time on their own side, and five spent most of their time on the conspecific's side (p = .041, binomial probability). Subjects spent significantly more time on their own paper towel than on that of the unfamiliar conspecific (t = 2.30, df = 19, p = .033).

Although subjects failed to discriminate between their own paper towel and those marked by conspecifics collected under the same rock, they preferred their own odors to those of neighbors and strangers. Moreover, they spent, on average, less time on their own side when presented with substrate marked by a neighbor than when presented with one marked by a conspecific collected from a distant home range. Overall, the magnitude of side preference significantly varied among the distance categories (F = 3.30, df = 2,57, p = .044) (Figure 1).

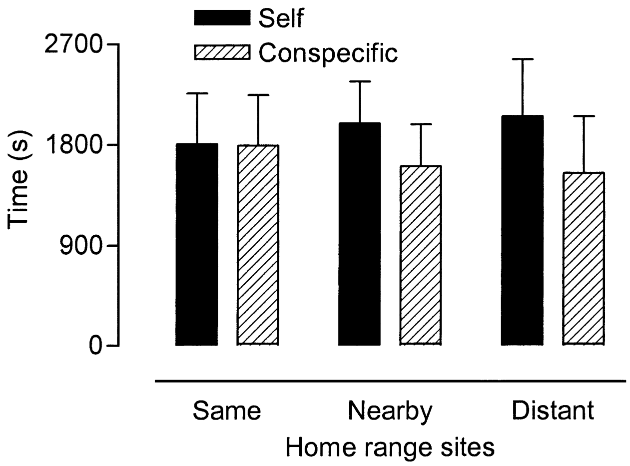

Figure 1
Time spent on substrate that subjects had marked themselves versus that spent on substrate marked by a conspecific (mean + SD) collected in the same home range (under the same rock), nearby home ranges (less than 5 m apart), or distant home ranges (more than 5 m apart).

Self/blank recognition

When given a choice between their own paper towel and a blank paper towel, which was moistened but never in contact with frogs, subjects generally preferred their own odor. Fifteen frogs spent most of their time on their own paper towel, and five spent most of their time on the blank paper towel ($p = .041$, binomial probability). Subjects spent more time on their own paper towel than on the blank paper towel ($t = 2.53$, df = 19, $p = .020$) (Figure 2).

Conspecific/blank recognition

When given a choice between a paper towel that had been marked by a conspecific and a blank moistened paper towel, subjects generally preferred the blank. Results of tests conducted with conspecifics collected less than and greater than 5 m from the test subject were very similar and thus were pooled to increase statistical power. Six frogs spent most of their time on the paper towel marked by the conspecific, and 14 spent most of their time on the blank paper towel ($p = .12$, binomial probability). Subjects spent more time on the blank paper towel than on that marked by the conspecific ($t = 2.15$, df = 19, $p = .045$) (Figure 2).

DISCUSSION

Our results demonstrate, for the first time, that adult anuran amphibians use chemical cues to communicate socially. Frogs perceived and responded to chemosignals that they had previously deposited on paper towels. These cues alone were sufficient to elicit discrimination between substrate occupied by self versus nonself. Moreover, responses to conspecifics were graded based on the extent of spatial overlap of individuals' natural home ranges. Frogs that were found co-occupying home ranges in the field failed to discriminate between self and conspecific chemosignals even after being held in separate containers for 72 h. Frogs showed stronger preferences for their own substrate, on average, when the conspecific to whose odors they were exposed had been collected farther away from their own home range (Figure 1).

Hamilton's frog is capable of self-recognition and can discriminate between neighbors and strangers. Individuals may express chemical signatures that consist of components that are genetically encoded, environmentally influenced, or a combination of both. In another study, Lee and Waldman (2002) found that fecal cues alone elicited self and neighbor recognition in this species. Differences in the availability of food items from one home range to another (Bell, 1995) might be sufficient to impart distinctive odors to frogs (Daly, 1995) or to their feces (Walls et al., 1989). To the extent that cues are genetically encoded, they would more directly reflect the unique identity of individuals. Yet, environmentally influenced odors also can be sufficient to encode individual identity (Halpin, 1986).

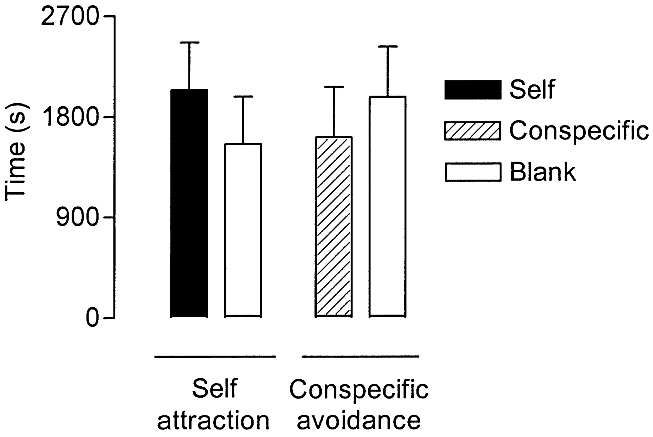

Figure 2
Time spent on substrate that subjects had marked themselves versus that they spent on blank substrate (mean + SD) (left), and time spent on substrate marked by an unfamiliar conspecific (collected at least 5 m away) versus blank substrate (mean + SD) (right).

The present study does not provide evidence of the function of social discrimination in Hamilton's frogs. Social recognition based on chemosignals might be useful in a variety of contexts. Besides discrimination of self from nonself, and neighbors from strangers (Jaeger, 1981), chemosignals may function to facilitate cooperation among close kin or selection of nonkin as mates (Madison, 1975). The avoidance of close inbreeding, or optimal outbreeding (Bateson, 1983), can be particularly important for species such as *L. hamiltoni* that live in highly structured genetic populations (Waldman and McKinnon, 1993). Based on our preliminary genetic results, we would not be surprised to find that individuals collected under the same rock were close kin and that coefficients of relatedness between conspecifics decline as a function of the distance between their home ranges.

Long-term field studies reveal that over their lifetimes, which can exceed 30 years (Bell, 1994; Bell BD, personal communication), *L. hamiltoni* demonstrates strong site fidelity (Newman, 1990). From year to year, many frogs can be found repeatedly under the same rocks. Frogs remain under rocks, logs, and litter during daylight hours but emerge during the evening and are active at night, particularly after rain moistens the forest floor and prey emerge. Our field observations suggest that individuals travel slowly over small home ranges and return to their daytime refuges as morning approaches. Frogs thus become familiar with the odors of their neighbors and learn to recognize chemical traces that mark their home ranges. Presumably, this ability enables frogs to recognize and respond appropriately to strangers that may be potential competitors or mates. Their chemosignals thus appear to form the basis of a communication system that enhances the fitness of the signalers (sensu Bradbury and Vehrencamp, 1998).

Frogs were attracted to the substrate that they had previously marked themselves but also avoided chemical cues deposited by unfamiliar conspecifics. Social discrimination may come about from a combination of attraction to familiar cues and repulsion from unfamiliar cues (Park and Propper, 2001; Waldman, 1986). Our results suggest, however, that both familiar and unfamiliar chemosignals are recognized. Differential responses elicited by familiar and unfamiliar chemosignals may be context-dependent. Within their home range, neighbors might accept one another but direct agonism toward intruding conspecifics. Conversely, reproductive individuals may approach potential mates that smell unfamiliar but may withdraw from those that smell familiar. We closely matched subjects' sizes in this study, but *L. hamiltoni* can assess the size of conspecifics by components of their chemosignals (Lee and Waldman, 2002). Sexual identity also is likely communicated through chemical cues, but we were unable to examine this owing to the sexual monomorphism and protected status of the species.

Chemosignals facilitate many forms of social communication in urodeles and apodans (for review, see Dawley, 1998; Madison, 1977), the other extant amphibian orders. Because of the high sensitivity and broad discriminability of their chemosensory systems, salamanders long have served as an experimental model for studies of olfaction (Kauer, 2002). Salamanders can differentiate between chemical signals of self and nonself (Gillette, 2002; Horne and Jaeger, 1988; Mathis, 1990; Simon and Madison, 1984), familiar and unfamiliar individuals (Jaeger, 1981), individuals from their own versus other populations (Evans et al., 1997; Rollmann et al., 2000), and conspecifics versus heterospecifics (Dawley, 1984; Jaeger and Gergits, 1979; Ovaska and Davis, 1992). Chemosignals deposited on substrates serve as territorial markers (Horne and Jaeger, 1988; Jaeger, 1986; Mathis, 1990; Ovaska and Davis, 1992) and communicate information about sex, body size, social status, and reproductive readiness (Dawley, 1984; Houck, 1986; Houck and Regan, 1990; Jaeger and Gergits, 1979; Mathis, 1990). Chemical signaling is used to attract mates (Arnold and Houck, 1982; Jaeger and Wise, 1991; Walls et al., 1989) and to recognize eggs (Forester, 1979, 1986; Forester et al., 1983). Caecilians also may communicate information on sex, reproductive state, and kinship by means of chemosignals, for territorial marking and mate choice (Warbeck et al., 1996; Warbeck and Parzefall, 2001).

Anuran secretory glands share features with those used for chemical communication by salamanders (Houck and Sever, 1994; Thomas et al., 1993). We currently are characterizing the chemical structure of the signals and identifying the glands that secrete them. Systems of chemical communication in amphibians show plasticity as a function of age (Chris, 1997; Hayward et al., 2000), sex (Dawley, 1984; Ovaska, 1988), season (Dawley, 1984; Madison, 1975), and stress levels (Mathis and Lancaster, 1998), all factors that will need to be considered in future studies of chemical communication in Hamilton's frogs.

Because the Leiopelmatidae represents the phylogenetically most basal lineage of anuran amphibians, our discovery of chemical communication in this group offers a window into how frogs may have communicated before mechanisms of bioacoustic communication evolved. Species that do not communicate acoustically may instead use pheromones for recruitment, defense, and mate choice. Communication by bioacoustic signaling can be energetically expensive (Bucher et al., 1982; Grafe, 1996; Wells and Taigen, 1986) and can incur risks (Ryan et al., 1981, 1982) that exceed costs associated with the production and use of chemosignals (Bradbury and Vehrencamp, 1998; Dicke and Sabelis, 1992; Zuk and McKean, 2000). Moreover, chemosignals may be better than acoustic signals at conveying many types of information. Chemosignals can encode high levels of specificity, can be expressed in a context-dependent manner, and can persist in the environment as long-lasting markers.

Sadly, systems of chemical communication may be especially vulnerable to disruption by anthropogenic change, such as exposure to pesticides, herbicides, and industrial pollutants (Park et al., 2001). Hence, an understanding of the mechanisms by which frogs use chemosignals, as well as their consequences with respect to survival, reproduction, and recruitment, may prove vital to the conservation of threatened species (Waldman and Tocher, 1998) such as Hamilton's frog. By suitably manipulating aspects of frogs' chemical ecology in captive rearing programs, we might accelerate rates of reproduction and facilitate progress toward species recovery.

Communication through other sensory modes, for example, by the use of visual (Haddad and Giaretta, 1999; Hödl and Amézquita, 2001; Lindquist and Hetherington, 1996; Summers et al., 1999), tactile (Heying, 2001; Ovaska and Rand, 2001; Seidel, 1999; Walkowiak and Munz, 1985), or seismic signals (Lewis and Narins, 1985; Narins, 1990) clearly also is possible. Nonetheless, given the utility of chemosignals as markers of home range, social status, reproductive condition, and individual identity (Alberts, 1992), we suggest that chemical signals may provide an important previously unrecognized mode of communication that may be common to many species of frogs and toads.

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