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Communication by Fecal Chemosignals in an Archaic Frog, *Leiopelma hamiltoni*

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Communication by acoustic signals has been extensively studied in anuran amphibians, but other sensory modalities have been largely ignored. We show here that the frog *Leiopelma hamiltoni* communicates through fecal chemosignals. When given a choice between their own and other individuals' feces, subjects spent more time near their own feces. Further, this effect was greatest when the conspecific was larger in body size, suggesting that information about size as well as individuality is communicated. Time spent near conspecific feces correlated negatively with the distance between the collection sites of the frogs. This correlation may reflect differential responses to the feces of frogs of varied levels of kinship and social familiarity: frogs may avoid nonrelatives and unfamiliar conspecifics. To test the hypothesis that frogs alter fecal production upon exposure to conspecific feces, we presented subjects with either one smear of their own and one smear of a conspecific's feces or two smears of their own feces. Frogs did not defecate more when exposed to conspecific feces. However, when the frogs did defecate, they placed their feces closer to the conspecific's feces than to their own. This supports our hypothesis that feces serve as signals to conspecifics. Visual and tactile cues were eliminated in our experiments. Our results show that the frog *L. hamiltoni* communicates with conspecifics through chemical signals. We suggest that chemical signaling may be widespread in anuran amphibians.

AMPHIBIANS use chemical cues for detecting prey and predators, homing and navigation, territorial defense, alarm signaling, mate choice, and social recognition (Dawley, 1998; Mason et al., 1998). Urodeles seem to rely much more on their chemical senses than do anurans (Jaeger and Forester, 1993), but perhaps only because chemical communication in urodeles has been more thoroughly studied. Most salamanders are quiet and secretive, unlike the vociferous frogs whose calls attract so much attention. Hence studies of anuran bioacoustics have contributed greatly to our understanding of mating systems (Wells, 1977), sexual selection (Waldman et al. 1992; Ryan, 1998), and speciation (Littlejohn, 1981; Gerhardt, 1994). Meanwhile, the possibility of communication through other means, such as the vibratory (Lewis and Narins, 1985; Narins, 1990), the visual (Summers et al., 1999; Hödl and Amézquita, 2001), and the chemical (Wabnitz et al., 1999; Pearl et al., 2000; Waldman and Bishop, in press) modalities, has been largely ignored. The absence of vocalizations in the social behavior of some anurans suggests that alternative means of communication exist.

Anurans are adept at using chemical cues in a variety of contexts. Some frogs and toads, even if blinded, orient to their breeding site, but anosmic individuals become disoriented, suggesting that orientation is based at least in part on chemical cues (Dole, 1968; Tracy and Dole, 1969; Sinsch, 1987). In controlled laboratory experiments, anurans respond to chemical cues from their home ponds (Grubb, 1973, 1976) and home areas (Forester and Wisnieski, 1991). Frogs respond not only to environmental chemical cues but also to chemosignals, such as sex pheromones (Wabnitz et al., 1999; Pearl et al., 2000). Larval anurans can detect and respond to predators based just on their chemical cues (Petranka and Hayes, 1998). When attacked by predators, some larval anurans release an alarm pheromone that induces defensive responses in conspecifics (Eibl-Eibesfeldt, 1949; Hews, 1988; Petranka, 1989). Larval anurans can recognize conspecifics (Kiseleva, 1996) and close kin (Waldman, 1985, 1986; Pfennig et al., 1994) based primarily on chemical cues. Postmetamorphic anurans also perceive and respond to chemical cues (Blaustein et al., 1984; Graves et al., 1993; Chivers et al., 1999). Yet the role of chemical communication in the social behavior of adult anurans has remained virtually unexplored (Waldman and Bishop, in press).

In contrast, chemical communication appears to be the key to understanding the social life of urodeles (Jaeger and Forester, 1993). Chemical signals facilitate individual spacing and mate choice in some species (Houck and Sever, 1994). Those salamanders deposit chemical signals on feces, conspecifics, and other substrates to communicate information about sex, body size, social status, and reproductive readiness. They can differentiate between chemical signals of self and nonself (Simon and Madison, 1984; Horne and Jaeger, 1988; Mathis, 1990), familiar and unfamiliar individuals (Jaeger, 1981), individuals from the same versus other populations (Evans et al., 1997), and conspecifics and heterospecifics (Jaeger and Gergits, 1979; Dawley, 1984). Chemical signals are used by both sexes to attract or coerce mates (Arnold and Houck, 1982; Walls et al., 1989; Jaeger and Wise, 1991). Some species care for offspring and recognize eggs by their chemical signals (Forester, 1986).

The Leiopelmatidae comprise the most ancient lineage of extant anurans, possessing characters found in Mesozoic fossils (Rocêk, 2000). Perhaps reflecting the ancestral state, they are largely silent (Bell, 1985) and are not known to communicate by vocalizing. Because they lack the external eardrums characteristic of modern frogs, their hearing lacks acuity (Wever, 1985). Morphological studies suggest that their vomeronasal and olfactory systems, however, are functional (Stephenson, 1951, 1955).

Leiopelma hamiltoni is similar in ecology to the species of salamanders that communicate chemically. Both inhabit the forest floor, rely on rocks, logs, and litter for cover and are active at night (Newman, 1990; Petranka, 1998). Both exhibit site tenacity and homing abilities (Madison, 1969; Newman, 1990). Vocalizations are not known to play a major role in conspecific communication in either group (Kiester, 1977; Bell, 1985; Petranka, 1998). Both care for eggs and young (Bell, 1985; Forester, 1986). Thus, we were prompted to investigate whether *L. hamiltoni*, like numerous salamanders, use fecal chemosignals to facilitate individual spacing.

Materials and Methods

Leiopelma hamiltoni is endemic to Maud and Stephens Islands in the Marlborough Sounds, New Zealand. This species is one of the rarest, most geographically restricted, and most vulnerable frogs in the world (Holyoake et al., 2001). Although Bell et al. (1998) classified Maud Island frogs as a new species (which they named *L. pakeka*), strong genetic similarities between the two populations contradict this view (Holyoake et al., 2001). We studied frogs on Maud Island during November 1999 and February 2000.

Frog collection and husbandry.—Test animals were collected from their diurnal refugia under rocks and were individually housed in 300 × 500-mm clear plastic bags with moist paper towels. Bags were inspected daily for feces. If feces were found, experiments were run that night. We conducted feces-choice experiments within at least three days of frog collection, and feces-production experiments within 30 h of frog collection. No frog was tested more than once. No frogs showed any obvious signs of stress or ill health. All frogs were returned to the precise locations of their capture at the completion of experiments.

As sex might be communicated through fecal chemosignals, which may possibly confound our results (see Mathis, 1990), we attempted to avoid opposite-sex pairings. Unambiguous determination of sex by currently available methods requires dissection, which is precluded by the frogs' vulnerable status. The adult size distribution is strongly bimodal, with females larger on average than males (Bell, 1978). Hence Bell (1995) defined individuals between 35 and 40 mm SVL as males, and those larger than 40 mm SVL as females. Of course frogs falling into the "male" category could be young females. Individuals smaller than 35 mm SVL were considered subadults. In our experiments, we matched frogs with others from within the same size class. This method is imperfect but was our best option. Results of tests on the three size classes did not differ and were therefore combined in statistical analyses.

Experimental apparatus and procedure.—We tested frogs in 33 × 20 × 8-cm clear plastic boxes, lined with clean moist paper towels. A self and a conspecific fecal pellet were placed at opposite ends of the box; placement was randomized to protect against side-bias. We removed potential tactile and visual cues by smearing the feces onto the paper towels lining the test box, and by conducting the first two observation periods in the dark. At each end of the box, we placed a shelter of white PVC tubing cut in half (80 mm length, 35 mm diameter). The shelters were positioned parallel to each other (modified from Jaeger et al., 1986).

To test the ability of *L. hamiltoni* to gain information from feces, we placed a single frog into the center of a testing box and allowed it to choose between the self and conspecific sides. Frogs were introduced into the box at sunset and were allowed to acclimate for 30 min. We then recorded the side of the box on which the frog was located once every 15 min from 30 min after sunset to 2.5 h after sunset ("evening"), from 4.5 h after sunset to 6.5 h after sunset ("night"), and from 1 h after sunrise to 3 h after sunrise ("morning"). Because of logistical constraints, some trials could not be continued to morning. Samples sizes for evening, night, and morning, respectively, were n = 26, 26, and 21. Plastic bags were used only once to avoid contamination. Plastic boxes were thoroughly cleaned with water and air-dried between trials.

To test whether frogs countermark in response to conspecific intrusions, we simulated intrusions by placing a smear of the subject's feces at one end of a testing box and a smear of a conspecific's feces at the other end (n = 8). As in the first experiment, placement was randomized. For the control, we placed smears of the subject's feces at both ends of a box (n = 8). We placed the subject into the box at sunset and stopped the experiment 30 min after sunrise. We recorded whether the subject defecated during the experimental period, the location of newly deposited feces, and the mass of the feces. Feces were placed into sealed 0.5 ml microcentrifuge tubes and wet mass was measured upon return to Christchurch.

Statistical analyses and predictions.—For the feces-choice experiments, we hypothesized that *L. hamiltoni* uses fecal chemosignals to facilitate individual spacing. Thus, like salamanders (Jaeger et al., 1986), *L. hamiltoni* should spend more time on the self side than on the side with the conspecific fecal smear. We determined how many frogs spent more than half their time on the self side and analyzed the data by comparison to a binomial distribution. We analyzed each time period (evening, night, morning) separately as well as the data summed over the entire experimental period. As we obtained the strongest results in the evening, we used the responses from this time period in the following analyses.

First, we examined whether body size is communicated through feces. We predicted that frogs exposed to the fecal smear of a larger conspecific (within their size class) would spend less time near that conspecific's fecal smear. We compared trials in which subjects were exposed to the fecal smear of a larger frog to trials in which subjects were exposed to the fecal smear of an equal-sized or smaller frog. We analyzed differences in the time spent on each side of the box between the two treatments with a two-sample t-test.

Tadpoles and froglets of some species of anurans prefer to group with close relatives (Waldman, 1991), while the "dear enemy" effect predicts that familiar neighbors will be tolerated more than strangers (Jaeger, 1981). In the field, both genetic relatedness and social familiarity probably decrease with distance between individuals [relatedness declines with distance in *L. archeyi* (BW, unpubl. data), a species very similar in ecology, behavior, and evolutionary history to *L. hamiltoni*]. Thus, we tested whether time spent on the conspecific side correlated negatively with the distance between the collection sites of the subject and the conspecific.

In the feces-production experiments, we tested whether frogs would countermark against conspecific signals (Mathis, 1990). We predicted that frogs exposed to both their own and conspecific feces would be more likely to defecate and would produce more feces than those frogs exposed to only their own feces. We compared the numbers of frogs that defecated during the experimental period with a χ^2 test of independence (with Yates correction for continuity). Because the distribution of fecal masses departed significantly from normality, we compared fecal masses with a Mann-Whitney U-test.

We also predicted that, if frogs countermarked, the newly defecated feces would be placed near the conspecific's feces. We subtracted the distance between the newly defecated feces and the conspecific smear from the distance between the newly defecated feces and the subject's own smear. Thus, positive differences describe frogs that placed their feces closer to the conspecific smear, whereas negative differences describe frogs that placed their feces closer to their own smear. Because the differences departed significantly from normality, we tested them against a null expectation of zero with the Wilcoxon signed-rank test.

Statistical tests were conducted by methods of Zar (1999), with Minitab 13.30 or SigmaStat 1.0. Statistical inferences are based on two-tailed alternative hypotheses. Means are presented ± SE.

Results

Choice tests.—Most frogs spent the majority of their time on the side with their own feces over the duration of the test (binomial test: P = 0.029). This tendency was strongest early in the test and decreased with time (Fig. 1).

During the period in which the response was strongest (evening), the time frogs spent on the conspecific side was negatively correlated with the distance between collection sites ($r_{17} = -0.60$, P = 0.008, Fig. 2). Further, subjects presented with feces of larger frogs (subject size–conspecific size $= -2.1 \pm 0.5$ mm) were less likely to spend time on the conspecific side than were frogs presented with the feces of equal-sized or smaller frogs (subject size–con-

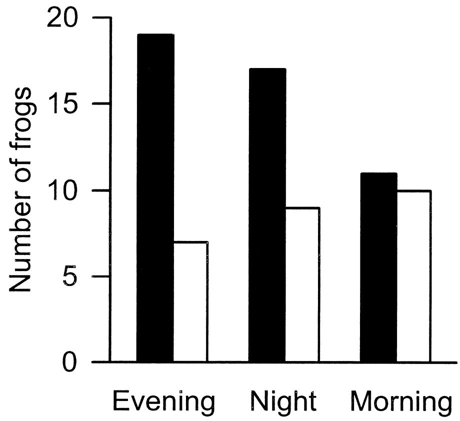

Fig. 1. Numbers of subjects that spent more than half their time on the side with their own fecal smear (black bars) or with the conspecific's fecal smear (white bars; evening: P = 0.029; night: P = 0.169; morning: P = 1.000; binomial tests). When data are analyzed over the duration of the night, subjects preferred their own smears (see text).

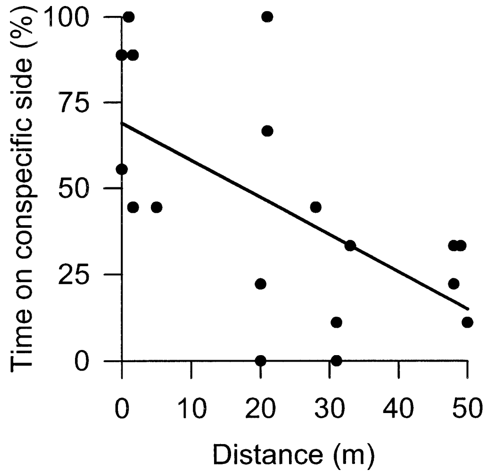

Fig. 2. Time spent on the side with the conspecific's fecal smear correlated negatively with the distance between the frogs' collection points.

specific size = 2.0 ± 0.4 mm; t_{24} = 2.29, P = 0.03; Fig. 3). Over the three size classes, subjects exposed to the feces of larger frogs did not differ in size from those of subjects exposed to equal-sized or smaller frogs (36.0 ± 1.3 mm vs 38.2 ± 1.2 mm, respectively; t_{24} = 1.22, P = 0.23).

Feces production tests.—Subjects were not more likely to defecate if exposed to conspecific feces. Ten of 20 frogs defecated in the experimental treatment, and eight of 20 frogs defecated in the control treatment (χ_1^2 = 0.012, P = 0.91). Subjects did not produce more feces by mass when presented with conspecific feces than when presented with just their own feces (medians: conspecific, 41.0 mg; own, 44.0 mg; Mann-Whitney U-test: T = 386, n_1 = 10, n_2 = 8, P = 0.52). When the subjects in the experimental treatment did defecate, however, they usually placed their feces closer to the conspecific's feces than to their own (medians: distance to conspecific, 4.8 cm; distance to own, 23.8 cm; difference, 19.0 cm; Wilcoxon signed-rank test: W = 33, n = 8, P = 0.042).

Discussion

Because we controlled for visual and tactile cues, the frogs' differential responses appear attributable to chemical signaling. The feces-choice results demonstrate that chemosignals varied among individuals and that frogs were able to gain information from and adjust their behavior according to those signals. The feces-production results show that frogs selectively deposit feces in response to conspecific signals.

As the experiments progressed from evening to morning, frogs' preferences for their own feces decreased. Feces may serve a social, communicatory function during the evening and night, when the frogs are active, but may fail to elicit a response in the morning, when they are normally inactive and under rocks. Moreover, chemical signals in the feces may have decayed with time, test subjects could have habituated to the signals, or test subjects may have transferred them around, thereby reducing the gradient across the testing apparatus. Further experi-

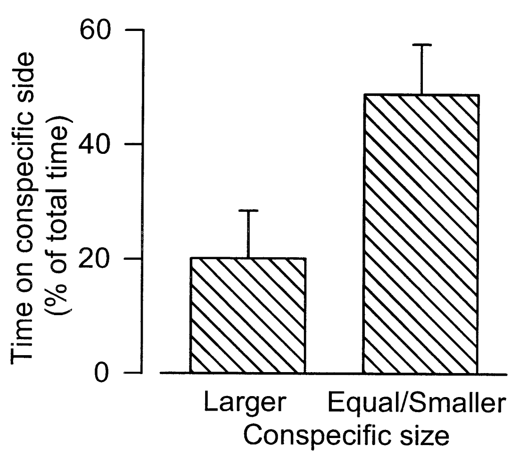

Fig. 3. Subjects spent less time on the side with the conspecifics' fecal smears if the conspecific was larger than if the conspecific was equal to or smaller than the subject. Mean (+ SE) percentages indicated.

ments are necessary to determine the significance of the temporal trend in side preferences.

Feces often are used to advertise home ranges and social status (Gosling, 1990; Aragón et al., 2000). *Leiopelma hamiltoni* may use feces in a similar manner. Frogs in the feces-production experiments defecated at all times, from evening to morning. If frogs do so in nature, they would mark their foraging areas because individuals (both subadults and adults) typically forage in the same location over multiple nights (Newman, 1990).

The feces-choice experiment suggests that intruders are repelled by feces if the resident is larger than the intruder. Our results do not reflect behavioral differences between small and large subjects per se. Rather, subjects may have assessed the conspecific's size from signals in the feces and adjusted their behavior accordingly. Body size emerges as a significant effect even though we tested subjects within defined size classes and despite the variation attributable to distances (see Fig. 2). This suggests that the communication of size plays an important role in the social interactions of *L. hamiltoni.* Size might indicate resource holding potential or genetic quality and could be maintained as an honest signal through correlations between body size and metabolism/gland activity or dietary differences (Zahavi and Zahavi, 1999). Indeed, changes in diet as a function of size have been well documented in frogs (e.g., Lima, 1998; Hirai and Matsui, 1999; Newman, 1999), as have dietary influences on glandular secretions (Daly, 1995).

The results also suggest that intruders from more distant locations would be repelled. At a mechanistic level, this could be caused by differential responses to familiar versus unfamiliar conspecific signals, by genetic or environmental influences on the signals, or both. Regardless of the mechanism, a correlation between familiarity, relatedness, and geographic distance in nature should allow kin- and neighbor-recognition (Waldman, 1987). Perhaps frogs are repelled by the signals of conspecifics from distant locations because they are ''unfamiliar enemies'' (Jaeger, 1981) or are less closely related. Although we did not test for mating preferences, kin recognition via chemical signals could also provide an avenue through which this nonvocalizing species may avoid inbreeding or optimally outbreed (Bateson, 1983).

When we simulated conspecific intrusion, subjects defecated near the intruder feces. Although we did not record side preferences in this experiment, we collected subjects from a mean distance of 61.19 ± 10.77 m from the collection sites of the conspecifics. Given this considerable distance, the correlation between time and distance in our choice experiment allows us to infer that most subjects probably spent the majority of their time near their own feces. That subjects still deposited their feces close to the intruder feces supports our hypothesis that feces are selectively placed to communicate with conspecifics.

We tried to avoid male-female pairings because our experiments centered on the recognition of home range. Future work on the role of chemical signals in intersexual encounters may reveal further similarities between anurans and urodeles (e.g., Mathis, 1990; Dawley and Crowder, 1995). Indeed, sex pheromones recently have been documented in other anurans (Wabnitz et al., 1999; Pearl et al., 2000).

Our work demonstrates that *L. hamiltoni* communicates through fecal chemosignals. Other chemical signals also may facilitate communication in this species (Waldman and Bishop, in press). The discovery of chemical communication in a species phylogenetically basal to most other anuran amphibians raises the possibility that this character is shared by many other frogs and toads. The chemosensory modality may be particularly important for species that do not communicate through acoustic signals. We suggest, however, that chemical signals may provide an important mode of communication even in those species that communicate acoustically. Chemosignals may serve as efficient, long-term markers of home range, social status, and individual identity, even as vocalizations communicate transitory information about the caller's condition and motivational state.

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