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FECAL SCENT MARKING IN THE WESTERN BANDED GECKO (*COLEONYX VARIEGATUS*)

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ABSTRACT: We examined the phenomenon of feces confinement in western banded geckos (*Coleonyx variegatus*). Discrete "defecatoria" (preferred defecation sites) were observed for both males and females housed individually. Lizards tended to establish defecatoria away from their own diurnal resting sites as well as areas marked by conspecifics. Geckos formed more compact defecatoria when introduced into an arena marked by a member of the opposite (versus the same) sex, suggesting the presence of sex-specific fecal cues. Responses to extracts of feces suggest that chemical cues are important in mediating defecation patterns and that geckos are able to recognize the scent of their own feces. Defecatoria may serve to reduce predation pressure or as social "signposts" where geckos obtain information concerning conspecifics.

Key words: *Coleonyx variegatus*; Chemical signal; Eublepharinae: Gecko

CHEMICAL signals are important in the spacing and social behavior of a variety of animals (Gosling, 1982; Stoddard, 1980). Many reptiles rely on the use of such signals in their life histories (reviewed by Mason, 1992), and lizards are no exception. For example, chemical cues are utilized by the skink *Eumeces laticeps* in discrimination of prey odors (Cooper and Vitt, 1986*a*, 1989), eliciting male courtship behavior (Cooper et al., 1986), and species identification (Cooper and Vitt, 1986*b,c*). Cooper (1989) concluded that the autarchoglossans *Heloderma suspectum* and *Varanus exanthematicus* rely on discrimination of prey odors in their foraging activities. Western banded geckos (*Coleonyx variegatus*) use chemical cues in sexual

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recognition (Greenberg, 1943), in acquiring information concerning conspecifics (Greenberg, 1943; J. Jenkins, unpublished data), and in detecting potential predators (Dial et al., 1989). Chemical signals, therefore, are likely to be important in many facets of the ecology of *C. variegatus*.

Lizards of the genus *Coleonyx* deposit feces in accumulative piles. For example, Jenkins (unpublished data) observed the formation of fecal piles ("defecatoria") by individually housed *C. variegatus*. Group-housed individuals of *C. variegatus* have been observed to share a common defecatorium (Jenkins, unpublished data; G. Carpenter, personal observation). This has also been observed in an allopatric congener, the Texas banded gecko (*Coleonyx brevis*) housed under semi-natural conditions (G. Carpenter, unpublished observation) and for other eublepharine geckos in zoos (J. Groves, personal communication; B. Bartholomew, personal communication). Defecatoria of *C. variegatus* (J. Jenkins, unpublished data) and *C. brevis* (personal observation) have been observed in the field as well.

Thus formation of defecatoria by *Coleonyx* appears to be a robust phenomenon. However, no quantitative analysis of this behavior has been done, nor have social influences on its expression been investigated. Therefore, we performed a series of experiments using *C. variegatus* to test the following hypotheses: H_1—individuals of *C. variegatus* confine fecal depositions to constricted areas, thus producing defecatoria; H_2—they share defecatoria, thus practicing communal defecation; and H_3—they use chemical cues to locate established defecatoria and may assess conspecifics via fecal olfactants.

An experiment was performed wherein we housed geckos individually and noted patterns of defecation. In a subsequent experiment, we introduced lizards into these previously marked arenae and noted their patterns of defecation to test the hypothesis of communal defecation. A third experiment with chemical extracts of feces was designed to obtain information on the importance of olfactory cues in mediating patterns of defecation.

Methods

General Methods

Adults of *C. variegatus* were obtained in May 1983 from Desert Specialties Incorporated, Riverside, California. During experimental trials, lizards were maintained individually in terraria (approximately 250 cm^2) and exposed to a 14L:10D photoperiod at 25 C. We placed a small cardboard shelter, a petri dish of water, and a small rock at each end of each terrarium. The objects were arranged so that opposite ends were visually equivalent. During experimental periods, we fed the lizards an ad libitum diet of crickets (to promote prolific defecation) and noted daily the diurnal resting site of each lizard. At the end of each experimental trial, we drew a defecatorium map by sketching the location of each fecal bolus deposited onto a scale map. A measure of defecatorium spatial compactness was calculated and served to provide a quantitative assessment of feces confinement.

We developed an index of the spatial distribution of deposited feces as a measure of defecatoria compactness and to provide numerical data for statistical analyses. Values of the Feces Confinement Index (FCI) were determined as follows. The most central fecal pellet in a defecatorium was visually determined, and the distances from this pellet to each other fecal pellet were measured to the closest millimeter (d_i). A d_i value of 1 mm was assigned to any pellet that came in contact with the most central one, because zero cannot be incorporated into the formula for FCI. The harmonic mean of the d_i values was used to calculate FCI. A harmonic mean is appropriate because a single outlying number (or fecal pellet) has a small effect on the yielded value (versus an arithmetic mean, for example).

The formula for calculating FCI is

$$FCI = \frac{1}{\frac{\Sigma(1/d_i)}{n-1}}.$$

We treated each value of FCI as a radius and determined a value for the percentage of total area available (floor area of the arena) occupied by the defecatorium (a circular area calculated from the radius). Smaller FCI values indicate more compact defecatoria.

Experiment 1

Nine males and nine females of *C. variegatus* were kept individually in study arenae for 2 wk and were then removed and their defecatoria mapped. We converted these data to FCI values and ran a chi-square analysis (Zar, 1984) as a test for significance of non-random fecal deposition.

Experiment 2

We performed this experiment to test the hypothesis of communal defecation. Six males and six females (the experimental group) were introduced individually into arenae that had been "marked" by a different set of six males and six females (the donor group) in Experiment 1. Three males and three females were introduced into male-marked arenae and the same numbers into female-marked arenae. After 2 wk, experimental lizards were removed from these arenae and their fecal depositions were mapped relative to those of the donor group (which could be differentiated using the previous map). We converted these data to FCI values and dealt with them as in Experiment 1.

We developed an index as a measure of discreteness of donor and experimental lizard defecatoria. Values for the Inter-defecatoria Index (IDI) were calculated by taking the distance between the two defecatoria (D) and dividing it by the average of the FCI values; D was calculated by measuring the closest distance between the two "circular" defecatoria formed by the FCI values (radii). The formula for calculating IDI is

$$IDI = \frac{D}{(FCI_1 + FCI_2)/2}.$$

An IDI value of zero indicated that circles formed around defecatoria by FCI values were precisely tangential to one another whereas a value of <0 indicated overlapping defecatoria. Because FCI values were slightly biased underestimates, defecatoria were considered discrete only when IDI values were >1. We employed one-way analysis of variance (Bruning and Kintz, 1977) to determine if marking was affected by the sex of the donor lizard.

Experiment 3

We performed this experiment to determine if geckos recognize and respond to fecal odors alone. Study arenae were rectangular plastic boxes with approximately 150 cm^2 of floor area, and they were arranged as in prior experiments. Fecal extracts were prepared using a 1:1 chloroform : methanol mixture. To prepare each extract, 2 ml of chloroform : methanol and a 0.5 g fecal sample were vortex-mixed for 60 s. We prepared two types of extracts. A mixed extract included the feces of several males and females, but never the feces of the lizard to be used in that trial. The other type of extract was made from the feces of the lizard to be used in that trial. At each end of the study arenae, either one of these extracts or the chloroform : methanol vehicle was applied to filter paper, and lizards were introduced after the solvent had evaporated. The three experimental conditions were (1) the lizard's own extract applied at one end of the arena paired with vehicle alone at the opposite end, (2) the lizard's own extract paired with a mixed extract, and (3) a mixed extract paired with vehicle alone. Original sample sizes were 10 lizards per condition, but a few lizards that were in poor health died during this experiment. The final sample sizes were eight lizards for condition 1, 10 lizards for condition 2, and seven lizards for condition 3. Lizards were kept in these arenae for 2 wk, then they were removed and we noted the position of deposited feces relative to location of extracts or vehicle. We calculated the mean number of fecal pellets at each end of the arena under each of the test conditions. Because sample sizes were small, data from males and females were pooled for statistical analyses. Three *t*-tests (Bruning and Kintz, 1977), for differences between two related

TABLE 1.—Feces Confinement Index (FCI) and percent area (%A) used for defecatoria in western banded geckos housed individually.

Males		Females	
FCI	%A	FCI	%A
7.28	0.092	9.72	0.165
8.05	0.113	19.11	0.634
13.61	0.325	20.31	0.720
26.61	1.24	20.37	0.724
30.11	1.58	21.61	0.815
31.44	1.72	23.92	0.999
51.36	4.06	25.76	1.16
65.63	7.52	30.86	1.66
73.10	9.33	65.80	7.57

means, were computed to compare the number of fecal pellets deposited at either end of the arenae under the three separate conditions.

RESULTS

Experiment 1

In all trials, discrete defecatoria were formed (Table 1). Mean FCI values were 34.1 ± 8.1 for males and 26.6 ± 5.3 for females. These values correspond to values of 2.9 ± 1.1% of available area (%A) for males and 1.6 ± 0.8%A for females. The least confined defecatorium was deposited by a male and yielded a FCI value of 73.1 (%A = 9.3). Although these markings were more scattered than those in all other trials, a chi-square analysis indicated that the distribution of feces was significantly nonrandom ($\chi^2_{(3)} = 27.45$, $P < 0.001$). A *t*-test indicated that FCI and %A values did not differ significantly between males and females. Defecatoria were established in shelters in 61% of the trials [5/9 (55%) of male and 6/9 (67%) of female trials]. This shelter was most often the one not used as a diurnal retreat.

Experiment 2

One-way analysis of variance indicated that both male and female lizards formed more compact defecatoria when introduced into an arena marked by a member of the opposite sex, versus the same sex ($F_{(1,11)} = 10.9$, $P < 0.05$). Feces confinement was observed in all trials, and the experimental defecatoria yielded smaller FCI values than did the donor defecatoria (Table 2). Experimental lizards established defecatoria in the shelters provided in each of the 12 trials. Values for IDI indicated that discrete defecatoria (IDI > 1.0) were established in 11 out of 12 cases. The smallest value for the 11 discrete pairs of defecatoria was 5.04, and most were much larger, indicating distinct separation of fecal piles. Chi-square testing did not support a hypothesis of communal defecation ($\chi^2_{2(1)} = 8.3$, $P < 0.01$).

TABLE 2.—Feces Confinement Index (FCI), percent area (%A) used, and Inter-defecatoria Index values for individual western banded geckos (experimental) introduced into arenae marked by donors. Values in parentheses are $\bar{x}$ ± 1 SE.

Donor sex	Experimental sex	FCI	%A	IDI
Male	Male	27.78	1.35	21.78
Male	Male	26.98	1.27	18.38
Male	Male	21.44	0.80	6.85
		(25.40 ± 1.99)	(1.14 ± 0.17)	(15.67 ± 4.52)
Male	Female	19.88	0.69	28.46
Male	Female	13.79	0.33	15.63
Male	Female	21.07	0.77	5.04
		(18.25 ± 2.25)	(0.60 ± 0.14)	(16.37 ± 6.77)
Female	Male	16.74	0.48	39.93
Female	Male	25.07	1.10	0.11
Female	Male	16.58	0.48	17.89
		(19.46 ± 2.8)	(0.69 ± 0.21)	(19.32 ± 11.52)
Female	Female	27.20	1.29	15.67
Female	Female	25.63	1.15	15.07
Female	Female	25.26	1.11	5.41
		(26.05 ± 0.59)	(1.18 ± 0.05)	(12.05 ± 3.32)

Experiment 3

Under experimental condition 1, both male and female lizards deposited a greater number of fecal pellets in the end of the arena where the extract of their own feces was applied than at the end where vehicle alone was applied (Table 3). A *t*-test indicated that these differences were significant ($t_{(7)} = 4.16$, $P < 0.01$). Under condition 2, no significant difference was found between the number of fecal pellets deposited at the end of the arena where a mixed extract was applied versus that of the lizards own feces ($P > 0.05$). Nevertheless, there appeared to be a trend for more feces to be deposited near the lizard's own fecal odor. Under experimental condition 3 (mixed extract paired with vehicle alone), the numbers of fecal pellets deposited at either end of the arenae were not significantly different. Defecatoria were located in shelters or adjacent corners in 76% of all trials (87.5% for condition 1, 70% for condition 2, and 71% for condition 3).

TABLE 3.—Defecatory responses of western banded geckos to study arenas with fecal extracts or control vehicle applied at opposite ends ($\bar{x} \pm 1$ SE).

Experimental condition	Number of fecal boli	
1. Own vs. vehicle	10.38 ± 1.24:2.25 ± 1.15	($n = 8$)
2. Own vs. mixed	7.10 ± 1.12:2.90 ± 1.13	($n = 10$)
3. Mixed vs. vehicle	4.86 ± 1.10:2.43 ± 0.97	($n = 7$)

DISCUSSION

We observed the establishment of defecatoria by *C. variegatus* in this study. Data from three experiments suggest that these lizards recognize and respond to fecal olfactants. Results from experiment 2 do not support the hypothesis of communal defecation, although some sharing of defecatoria has occurred under non-experimental conditions. These conditions involve the housing of several geckos in a common terrarium, conditions which were not repeated in this experimental protocol.

There are several possible functions of defecatoria including the following. First, defecatoria may reduce predation pressures. Defecatoria in this study were generally deposited in shelters at the opposite end of the study arena from the favored diurnal resting site. Geckos that spend less time in the vicinity of their feces would have a selective advantage if predators use olfactory cues. Second, western banded geckos appear to obtain olfactory information from feces, and concentrations of feces may provide a stronger chemical message than individual fecal pellets. Furthermore, depositing such a signpost in a sheltered area would lengthen the life of the signal. The few defecatoria observed in natural habitats have been in sheltered sites (Jenkins, unpublished data; G. Carpenter, personal observation for *C. brevis*). As in our study with *C. variegatus*, red-backed salamanders (*Plethodon cinereus*) have been reported to exhibit olfactory discrimination between feces of individuals (Jaeger et al., 1986; Horne and Jaeger, 1988). Pheromones, including fecal olfactants, in these salamanders are inferred to serve as territorial advertisements and facilitate "dear enemy" recognition (Jaeger, 1981, 1986) wherein individuals behave more aggressively towards strangers than towards familiar neighbors. Similarly, fecal olfactants in *C. variegatus* may allow individuals to sense the presence of strange and familiar conspecifics without physically proximate encounters. Third, defecatoria are usually established in hidden areas and they may be consequences of the evolution of thigmotactic (body-substrate) thermoregulation. A lizard's digestive rate increases with temperature (Harlow et al., 1976) and diurnal lizards often deposit feces in open areas where they bask (Auffenberg, 1978; Duvall, 1979, 1982). Nocturnal geckos acquire heat from the the substrate (Bogert, 1949; Dial, 1978; Marcellini, 1976), and geckos feed at night when air temperatures are lower than the average temperatures of diurnal retreats in rock cover. Therefore, they attain maximum temperature and digestive rate upon returning to the sheltered sites where they defecate. The fecal accumulations then function as social signposts.

The formation of fecal piles appears to be a reliable phenomenon in the genus *Coleonyx*, and likely in the gecko subfamily Eublepharinae. As these nocturnal animals rely on chemical information in certain facets of their life history (for example, see Dial et al., 1989; Greenberg, 1943), it seems probable that feces-derived chemical cues also play important roles. Defecatoria likely provide long lasting signals from which conspecifics derive information about one another.

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