



Intraspecific Chemical Communication by a Territorial Salamander via the Postcloacal Gland

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INTRASPECIFIC CHEMICAL COMMUNICATION BY A TERRITORIAL SALAMANDER VIA THE POSTCLOACAL GLAND.—

Adults of the terrestrial red-backed salamander (*Plethodon cinereus*: Plethodontidae) are territorial, as demonstrated by experiments both in the laboratory (Jaeger, 1981; Jaeger et al., 1982) and in a natural habitat [under cover objects on a forest-floor in Virginia (Mathis, 1990)]. Territories are advertised by pheromones (chemical signals) that are placed directly on the substrate (Jaeger and Gergits, 1979) or on fecal pellets by males (Jaeger et al., 1986) and females (Horne and Jaeger, 1988). Pheromones allow individuals to recognize each other uniquely (Jaeger, 1981) and to inform a potential intruder that a marked area contains a resident capable of defending it (reviewed in Jaeger, 1986). Residents and intruders nose tap substrates and fecal pellets (Jaeger, 1984), and apparently pheromones thereon are conducted from the nasolabial cirri (Jaeger, 1986) through the nasolabial grooves and nares, stimulating

receptors in the vomeronasal organs (Dawley and Bass, 1988).

One problem in furthering the study of territorial communication in salamanders has been uncertainty as to the source(s) of territorial pheromones. Are pheromones produced by nonmodified integumental (mucous and serous) glands, by specialized glands in the integument (e.g., analogous to the caudal hedonic glands that are used in courtship; Sever, 1989), by specialized glands in the cloaca, or by breakdown products of the feces per se? Simon and Madison (1984) and Jaeger (1984) believed that glands in the cloaca produce territorial pheromones, and Jaeger (1984) mistakenly (Simons and Felgenhauer, 1992) described "cloacal tapping" as a means by which red-backed salamanders place pheromones on the substrate.

Simons and Felgenhauer (1992), however, have histologically distinguished a complex of simple acinar glands that occurs posterior to the cloaca of *P. cinereus*, which they named the postcloacal gland. Their behavioral tests showed that males spent significantly more time investigating swabs rubbed over this gland (from other males) compared to control swabs. They consequently suggested that the postcloacal gland (not the cloaca) is one source of territorial pheromones and that secretions from this gland are placed on the substrate (by "postcloacal press") and on fecal pellets as territorial advertisement.

We tested this inference by Simons and Felgenhauer (1992) as part of our larger experiment on the influence of territorial quality (food types) on agonistic behavior by territorial residents and intruders. We knew from prior work (Gergits and Jaeger, 1990) that individuals of *P. cinereus* often nose tap each other during territorial conflicts. We, therefore, hypothesized that, if the inference by Simons and Felgenhauer is correct, then nose taps would be preferentially directed toward the area of the opponent's body containing the postcloacal gland.

Materials and methods.—Adult males of *P. cinereus*, all with tails intact (no autotomization), were collected at Hawksbill Gap off of Skyline Drive (Blue Ridge Mountains), Shenandoah National Park, Virginia, in Sept. 1991. They were returned to the laboratory, housed individually in petri dishes (14.0 × 1.5 cm) with one layer of damp filter paper, kept at 16 C with a 12L:12D photoperiod, and fed *Drosophila virilis* ad libitum until utilized in the experiment (Dec. 1991–March 1992). We report here only those methods of the experiment applicable to testing the hypothesis stated above.

Males were grouped by snout-vent length

TABLE 1. NUMBER OF TIMES THAT RESIDENTS AND INTRUDERS TOUCHED EACH OTHER WITH THEIR NASOLABIAL CIRRI. (A) All touches combined (including repeated touches by individuals) and (B) first touch only, with chi-square statistic. Segment 4 contains the postcloacal gland.

	Body segment				
	1 (head)	2 (fore-trunk)	3 (hind-trunk)	4 (fore-tail)	5 (hind-tail)
A. All touches					
Resident	8	4	3	20	19
Intruder	8	2	3	30	8
B. First touch					
Resident*	4	2	1	13	6
Intruder**	7	2	1	13	3

* $\chi^2 = 17.46$, $df = 4$, $P < 0.01$, two-tailed, $\alpha = 0.05$.

** $\chi^2 = 18.61$, $df = 4$, $P < 0.001$, two-tailed, $\alpha = 0.05$.

(SVL) and then were randomly paired, within groups, such that a future territorial resident and future intruder differed by no more than 2 mm SVL. We, thus, attempted to eliminate body size as an asymmetry in the forthcoming territorial contest (Maynard Smith and Parker, 1976). Each member of a pair was placed in a separate, but identical, chamber ($31.5 \times 17.0 \times 1.0$ cm) with a sheet of damp paper towel on the substrate and a glass lid. The future intruder was fed *Drosophila virilis*; the future resident was fed ants (*Solenopsis molesta*) or termites (*Reticulitermes*) or a combination of both, thus varying territorial quality for the resident (Walls et al., 1989). For purposes of testing our hypothesis, we do not differentiate among these feeding regimens. The salamanders were fed every second day in their chambers, were kept on a positive energy budget, and were maintained for six days at 16–21 C on a 12L:12D photoperiod. Six days provided adequate time for the salamanders to establish territories by marking them with pheromones (Jaeger, 1981).

On the sixth day (1400–1800 h), the resident was removed from and returned to his own chamber, being placed under a habituation lid (5.0×1.0 cm) on a randomly chosen end of the chamber; the intruder was removed from his chamber and was placed in the resident's chamber under an identical habituation lid on the opposite end of the chamber. After 15 min of habituation, the two males were released, and we monitored their interactions for 30 min. We conducted 51 paired trials.

We noted each time that a resident touched the intruder, or that the intruder touched the resident, with his nasolabial cirri (termed "touch"). We also noted the area of the oppo-

nent's body that was touched. To do this, we visually partitioned the body into five equal segments: (1) from the snout to the posterior articulation of the front limbs with the body, (2) progressively to the midtrunk, (3) to posterior of the cloaca, (4) to the proximal half of the tail (which contains the postcloacal gland), and (5) to the distal half of the tail. Our prediction, based on Simons and Felgenhauer (1992), was that most touches would occur at segment 4.

We also recorded as "contact" any physical meeting of the resident and intruder (excluding a bite), whether or not it involved the nasolabial cirri. We could then investigate whether contacts were related to the propensities of the 51 paired residents and intruders to bite. Such a comparison could not be made with "touch" per se, because the 26 paired contests involving touch yielded insufficient bites for analyses.

Results.—The 51 paired trials yielded a total of 54 touches with the nasolabial cirri by residents toward intruders and 51 such touches by intruders toward residents (Table 1A). The residents showed preferences for touching both segments (4 and 5) of the intruders' tails whereas the intruders showed clear preferences for touching the proximal segment (4) of the residents' tails. These data cannot be analyzed statistically due to multiple touches by some individuals, so we recast the data to reflect only the first touch by a resident toward his intruder or by an intruder toward the resident.

There were 26 first touches by the residents and 26 first touches by the intruders (Table 1B). Using one-sample chi-square tests (Siegel, 1956), the residents exhibited a significant deviation from equiprobable touches to the five segments of the bodies of intruders; segment 4 received 50% of the first touches. The intruders also deviated significantly from equiprobable first touches, and segment 4 received 50% of those touches as well. These data suggest that both residents and intruders prefer to investigate with their nasolabial cirri that portion of the opponent's body containing the postcloacal gland.

Our observations indicated that at least six intruders attempted to come into intimate contact with the postcloacal glands of residents. These individuals, when touching segment 4 with their nasolabial cirri, shoved their snouts under the tails of the residents, as if trying to lift the tails, and placed their snouts at the position of the postcloacal gland. Two individuals continued to hold their snouts in this position when the residents moved away, following in parallel snout-to-gland for several seconds.

Residents bit (1–35 times) in 37% of the trials

whereas intruders bit (1–46 times) in 10% of the trials (Table 2A–C), and contacts occurred in 75% of the trials (Table 2A–B, D). Both residents and intruders deviated from equiprobable distributions of behavior patterns shown in Table 2. The important points are that (1) 25% of the residents and 24% of the intruders failed to engage in contact (Table 2C, E) and (2) if a contact occurred early in the contest, it resulted in a bite 10% of the time (Table 2A) and no bite 51% of the time (Table 2D) for residents and for intruders 4% and 69%, respectively. It was relatively rare that a resident or intruder would bite first and then engage in contact (14% and 2%, respectively: Table 2B), but residents were seven times more likely to launch such a lightning attack. We infer, then, that a contact (which often involved a touch with the nasolabial cirri) tended to reduce escalation of a territorial conflict to the biting stage.

Discussion.—Our data demonstrate that territorial male residents and intruders of *P. cinereus* aim their chemosensory investigations of each other at that portion of the body containing the postcloacal gland. This provides support for the assertion by Simons and Felgenhauer (1992) that the postcloacal gland in this species is involved in territorial advertisement. Furthermore, our data suggest that early contact (which may involve pheromonal evaluation) between residents and intruders lessens the likelihood of biting, especially by intruders.

Simons and Felgenhauer (1992) suggested that the secretions from the postcloacal gland may provide individually unique signals, such that each salamander may have a different odor. In this way, the odor emanating from the postcloacal gland of a territorial resident and the odor previously placed by that gland on the substrate would provide consistent information to an intruder about the identity of the resident. Our data (Table 1A) suggest that intruders, more than residents, repeatedly assess chemical information from this gland, as predicted by Simons and Felgenhauer (1992). Our data do not indicate why residents might be interested in examining the postcloacal gland of intruders, which they frequently do, unless this gland conveys information beyond that of territorial ownership, such as neighbor (Jaeger, 1981), sexual, or kinship identification, or assessments of “fighting abilities” of intruders (Wise, 1991). Parallel studies with females of *P. cinereus*, which are also territorial, have yet to be conducted.

It is not yet clear whether the postcloacal gland is the sole source of chemical information utilized in advertising territories by males of *P.*

TABLE 2. INTERACTION OF CONTACT AND BITING. The number of times that residents and intruders (A) contacted before biting, (B) bit before contact, (C) bit with no other contact before or after, (D) contacted with no bite before or after, and (E) neither contacted nor bit. Residents ($n = 51$) and intruders ($n = 51$) were counted only once per trial.

	Number of behaviors by	
	Resident*	Intruder**
A. Contact before bite	5	2
B. Bite before contact	7	1
C. Bite, no other contact	7	2
D. Contact, no bite	26	35
E. No contact, no bite	6	11

* $\chi^2 = 30.85$, $df = 4$, $P < 0.001$, two-tailed, $\alpha = 0.05$.

** $\chi^2 = 81.84$, $df = 4$, $P < 0.001$, two-tailed, $\alpha = 0.05$.

cinereus. Simons and Felgenhauer (1992) reported that males also responded to secretions from the serous glands on the shoulder, to fecal material taken directly from the colon, and to secretions from the urinary collecting ducts. Thus, chemical communication in this species may be complex, with the postcloacal gland providing only a subset of information concerning territorial ownership.

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POSTPRANDIAL THERMOPHILY IN ROUGH GREEN SNAKES (*Opheodrys aestivus*).—Body temperature (T_b) varies with nutritional status in some reptilian species but not in others (Lillywhite, 1987; Sievert, 1989). Data on postprandial thermophily in snakes is limited to a few genera (Sievert, 1989). These snakes ingest large meals and then do not feed for several days or longer. We wanted to determine whether a snake that eats on a more frequent

basis, such as *Opheodrys aestivus*, would exhibit postfeeding thermophily. Unlike snakes that ingest large meals and experience extremes ranging from recent feeding to an extended fast, 86.7% of *O. aestivus* in the field had recently fed (Plummer, 1981). Although these feeding habits are atypical for snakes (Plummer, 1991), we hypothesized that the thermal behavior of *O. aestivus* would be similar to that of other snakes and that they would display postprandial thermophily.

Rough green snakes (*O. aestivus*) are diurnal, arboreal, and eat small, frequent meals consisting mainly of arthropods (Plummer, 1981). We determined the effect of feeding on T_b , and the effect of time of day on temperature selection in both fed and fasted *O. aestivus*. We hypothesized that *O. aestivus* would elevate its T_b after feeding and maintain constant T_b s throughout a 24-h period in a thermal gradient.

Materials and methods.—*Opheodrys aestivus* (22.0 ± 2.6 g) were captured in Charleston County, South Carolina, and maintained in the laboratory on a 12L/12D photoperiod (centered at 1200 EST) at 25 ± 1 C for three months. Snakes were fed gray crickets (*Acheta domestica*) every other day and given water ad lib.

Before scotophase on the day prior to the experiment, each snake was placed in a linear thigmothermal gradient and was allowed to habituate to the gradient. Each gradient was 150 cm long, 20 cm wide, and covered with a clear acrylic lid. The floor of the gradient was a 0.3 cm aluminum plate. Floor temperature ranged from 12 ± 3 C at one end to 45 ± 1 C at the other. An overhead fluorescent light source was on the same photoperiod to which the snakes were acclimated.

On the day of the experiment, a flexible Chromega-Alomega [(TM), Omega Engineering, Inc.] thermocouple was inserted 2 cm into the snake's cloaca, and the exiting wire was taped to the snake's tail. Cloacal temperatures were recorded at 10-min intervals for 24 h starting between 1000 and 1400 h. Only one snake was in a thermal gradient at a time. Cloacal temperatures were recorded on a Kane-May 1242 Digital Data Logger.

Snakes were not given food for five days prior to the experiment. Seven snakes were in a post-absorptive state during the experiment, and seven snakes were fed to satiation one to two h before the experiment. Each snake ate at least two adult crickets. The mean number of food items in the stomachs of wild *O. aestivus* is three (Plummer, 1981). All snakes were provided with water throughout the experiment. Data were