Pheromonal Self-Recognition in Desert Iguanas

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PHEROMONAL SELF-RECOGNITION IN DESERT IGUANAS.—Among vertebrates, there are many examples of chemical communication systems in which the presence and relative concentration of pheromone components varies among individuals. Intraspecific differences may be useful in social communication, potentially providing information regarding individual identity, sex, reproductive state, and social status. A common function of scent marking in vertebrates is to advertise territorial ownership. Such signals could be based on either a system of individual recognition combined with the ability to learn the status of conspecifics through repeated encounters, or a system of self-recognition combined with a scent-matching mechanism, in which the odors of self and any conspecifics encountered are compared to scent marks in the immediate vicinity (Gosling, 1982, 1986).

Many lizards possess specialized femoral glands on the ventral surface of the hindlegs that are controlled by androgenic hormones (Chiu et al., 1970, 1975; Fergusson et al., 1985), are more developed in males than in females, and are most active during the breeding season (Cole, 1966). Behavioral studies with iguanids indicate that femoral gland secretions elicit chemosensory investigation (Alberts 1989a; Duvall, 1986), although their precise functional significance remains undocumented. Chemical studies have shown that they are mostly composed of proteins (Cole, 1966; Fergusson et al., 1985; Alberts, 1990) that vary in composition both within and between species (Alberts, 1991). Although femoral gland secretions also contain some lipid material, no intraspecific variation in lipid components has been detected (Alberts, 1990; Weldon et al., 1990). Variability in the protein components of femoral gland secretions suggests that they could be useful in social communication. Although the extremely low volatility of proteins precludes detection by nasal olfaction (Wilson, 1970), perception could occur via the vomeronasal system (Halpern, 1987), which is highly developed in many lizards (Burghardt, 1970; Parsons, 1970).

Evidence from field studies suggests that, in desert iguanas, *Dipsosaurus dorsalis*, femoral gland secretions probably function in home range advertisement (Alberts, 1989b). Although the low volatility of femoral gland proteins increases their utility as signals of home range occupation, it has probably resulted in the need for initial signal localization by visual rather than olfactory cues (Duvall et al., 1987; Alberts, 1989a). If these secretions communicate territory ownership, then a recognition mechanism for perceiving this information must exist. Glinski and Krekorian (1985) have shown that desert iguanas are capable of distinguishing familiar from unfamiliar conspecifics under natural conditions and suggested that this ability is based at least in part on chemosensory cues. To examine the hypothesis that male desert iguanas can distinguish their own scent from that of other males, I compared the responses of male desert iguanas to their own secretions with their responses to secretions from unfamiliar male conspecifics.

Materials and methods.—In June, 1987, 10 adult male desert iguanas were captured in the Coachella Valley, Riverside County, California, and subsequently housed in two 1.2 × 0.5 × 0.5 m enclosures, each containing five males. The lizards were maintained on a 12:12 hour light cycle from 0700 to 1900 at a constant room temperature of 28 C and fed a variety of fresh fruits and vegetables three times a week. Additional heat was supplied by two heat lamps suspended above each enclosure. Two days prior to testing, a small sample of femoral gland secretion was collected from each male by applying gentle pressure around the gland openings and removing two to three secretion plugs with small forceps.

For each behavioral test, a lizard was placed in a clean enclosure (80 × 80 × 80 cm) and allowed to habituate for 3 min. A 0.5 mg secretion sample was rubbed onto a plastic tile (2 cm diameter) in the center of the enclosure. The lizards' behavioral responses were recorded on videotape for 15 min. The lizards were tested once per day over two days, from 1030 to 1300. The temperature of the arena was kept constant at 32 C, and the order of presentation of own versus unfamiliar secretions was randomized. Five of the lizards received their own secretions in the first trial, and five received secretions from the unfamiliar male first. In each

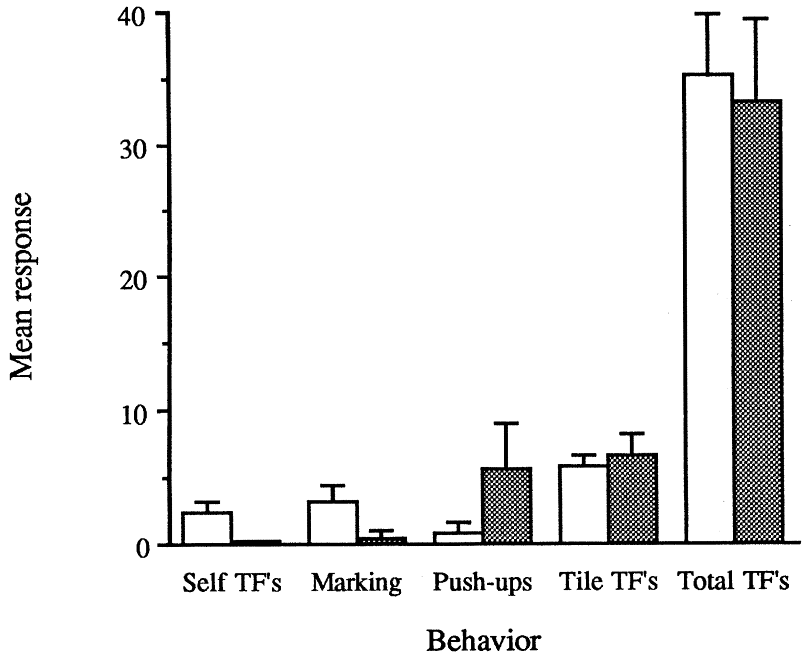

Fig. 1. Comparison of tongue-flicking (TF), marking, and push-up display behavior of 10 male desert iguanas in response to their own femoral gland secretions (open bars) and those of an unfamiliar conspecific male (shaded bars). Standard errors are given.

case, the unfamiliar secretions were taken from the largest male in the enclosure other than the one the test animal inhabited. The frequency of tongue-flicking, marking, and push-up display behavior was recorded for each test. Marking was defined as the lizard slowly dragging its hindlegs, cloacal, and tail region over the test tile. Desert iguanas have been observed in the field to mark small rocks in this manner (Alberts 1989b).

Results and discussion.—Results of the experiment are shown in Figure 1. When presented with their own secretions, eight of the 10 males tongue flicked their own tails at least once after tongue flicking the secretion tile. This behavior was never observed when the lizards were presented with secretions from the unfamiliar male (Fisher's exact test, $P < 0.01$). The difference in the number of tongue flicks males gave to their own tails in the presence of their own and unfamiliar secretions was highly significant (Wilcoxon T = 0.62, n = 10, $P < 0.005$). In addition, six of the eight lizards that tongue flicked their own tails also marked over their own secretions, whereas only one lizard marked in response to the unfamiliar secretions (Fisher's exact test, $P < 0.10$) and did so only once. When presented with his own secretion, this individual marked the tile a total of 13 times. The frequency of marking by lizards was significantly higher in response to their own than to unfamiliar secretions (Wilcoxon T = 3.61, n = 10, $P < 0.02$). There was a trend for males to direct more push-up displays toward the unfamiliar secretions, but only three males performed this behavior during the tests, and the difference between treatments was not statistically significant (Wilcoxon T = 11.26, n = 10, $P > 0.10$). Overall levels of chemosensory investigation, as measured by tongue flicks to the secretion tile (Wilcoxon T = 22.85, n = 10, $P > 0.50$) and total tongue flicks (Wilcoxon T = 24.00, n = 10, $P > 0.50$), did not differ significantly between treatments.

The observed behavioral differences between treatments indicate that male desert iguanas are capable of detecting and responding differentially to their own femoral gland secretions and those of unfamiliar conspecifics. Similar abilities have been demonstrated previously in blue-tongued skinks, which can discriminate their own odors from those of conspecifics (Graves and Halpern, 1991). That desert iguanas sometimes tongue flicked their own tails during the tests is highly suggestive of a scent-matching recognition mechanism analogous to that proposed by Gosling (1982) for mammals. Both active and passive self-marking in which scent gland secretions are spread over the body are common in mammals (Eisenberg and Kleiman, 1972) and may also occur in desert iguanas. Desert iguana femoral gland secretions are highly fluorescent under longwave ultraviolet light (Alberts, 1990). When a desert iguana with active glands is viewed under an ultraviolet light, fluorescence is not only visible in the glands but also is often detectable on the lower abdomen, around the cloacal region, and on the underside of the tail, indicating that secretions are not isolated within femoral glands but are spread over the lower body. Desert iguanas tongue flicked themselves when presented with their own secretion significantly more often than when presented with the unfamiliar secretion, suggesting that scent-matching may be relatively more important in situations that demand fine discrimination and that desert iguanas may be aware of the odor of their own secretion. When the desert iguanas in the experiment detected secretions in a novel environment that closely matched their own odor, they may have subsequently tongue flicked themselves to compare the two secretions directly.

Although examples of an animal marking in response to its own odor are common, marking in response to conspecific odors also occurs frequently (Eisenberg and Kleiman, 1972; Erlinge et al., 1982). The finding that desert iguanas marked significantly more often when presented with their own secretions suggests that marking behavior may be context dependent. Detection of its own secretions could serve to reassure a lizard and identify an area as "home," as has been proposed for mammals (Ralls, 1971; Johnson, 1973; Halpin, 1980), whereas marking may be inhibited when a lizard perceives it is in the territory of an unseen conspecific.

Despite divergence in the lizards' behavioral responses to their own versus unfamiliar secretions, overall levels of chemosensory investigation, as measured by tongue flicks to the secretion tile and total tongue flicks, were not significantly different between treatments. This lack of a difference in the level of investigation of two odors, despite sometimes dramatic differential responses in other behaviors, has been found in studies of mammalian recognition pheromones (Mykytowycz, 1975; Epple, 1978; Martin and Beauchamp, 1982). Although many past studies of lizard chemoreceptive abilities have relied on differential tongue-flicking rates as the criterion for discrimination between stimuli (Simon, 1983; Cooper and Vitt, 1986), results of this study suggest that such an approach may sometimes be too simplistic (but see Graves and Halpern, 1991) and that behavioral responses other than intensity of investigation should also be monitored.

Although results of this study are suggestive of a scent-matching recognition mechanism, they are consistent with the existence of either self- and/or individual recognition abilities and provide no means for distinguishing between them. Whether or not the information contained in femoral gland secretions can also be used in individual recognition remains to be investigated, but if an important function of these secretions is for a territory owner to communicate occupation of an area to potential intruders, then a recognition system based on self-recognition and scent-matching alone may be adequate.

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GENETIC UNIFORMITY IN THE JAPANESE GIANT SALAMANDER, *ANDRIAS JAPONICUS.*—The family Cryptobranchidae includes two extant genera, the American *Cryptobranchus* and Asian *Andrias* (Frost, 1985). Of these, the American hellbender, *Cryptobran-*