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# SOCIAL SIGNIFICANCE OF SCENT MARKING IN CAPYBARAS

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Capybaras, *Hydrochaeris hydrochaeris*, scent mark with a sebaceous snout gland and anal glands, either separately or in sequence. In the Venezuelan llanos, marking was observed 3,864 times. A minority of marks was associated with aggressive interaction, but most marks were deposited out of any obvious context. Males marked more often than females, and the majority of marks with the snout gland was followed by marks with anal glands. Rates of marking by individuals were associated with social rank and decreased with group size.

**Key words:** scent marking, capybaras, *Hydrochaeris hydrochaeris*, scent glands, dominance, aggression, territoriality

Social odors can convey a wide range of information (e.g., Brown, 1979; Müller-Schwarze, 1983), sometimes linked to agonistic behavior in ritualized contests over resources (e.g., Gosling, 1990). They also can indicate group membership, as in matrilineal cats, *Felis sylvestris catus* (Pasanisi and Macdonald, 1990), or individual identity, as in dwarf mongooses, *Helogale undulata* (Rasa, 1973). Frequently, scent-marking behavior and the chemistry of the secretion are related to social dominance (e.g., Huck and Banks, 1982; Novotny et al., 1990; Ryon and Brown, 1990). In capybaras, *Hydrochaeris hydrochaeris*, scent marking is common (Azcárate, 1980), and the scent glands are well described (Macdonald, 1985; Macdonald et al., 1984). However, the social context of marking has not been described in detail, and its function is unknown.

Capybaras, 50-kg grazing hystricomorph rodents of neotropical, seasonally flooded savannas, possess two scent glands. One, the morrillo, is an oval-shaped, shiny protuberance on top of the snout (Rewell, 1949) and is highly developed in males but, although detectable, virtually invisible in females (Macdonald et al., 1984). For this

reason, its presence can be used to distinguish adult males from females in the field. The other gland consists of a pair of pockets located next to the anus. Anal glands are developed in both sexes. In males, the pocket is mostly dry with modified hairs (osmetrichia), while females' pockets are coated with a greasy smear (Macdonald et al., 1984). A typical marking sequence for males involves rubbing the morrillo against a shrub or twig, then straddling the plant, pressing the anal pocket onto it, and, at least sometimes, simultaneously urinating on the plant (Azcárate, 1980; Macdonald, 1985; Macdonald et al., 1984). The morrillo and anal glands also may be used in separate scent-marking patterns.

Capybaras in our study area live in mixed-sex groups composed of ca. 10 adults of both sexes and a variable number of young-of-the-year (Azcárate, 1980; Herrera and Macdonald, 1987; Macdonald, 1981). Membership of these groups is quite stable, with few changes occurring even across years (Herrera and Macdonald, 1987). The mating system is polygynous within each group. Males form a stable dominance hierarchy that is extremely well defined by results of interactions between

dyads, with dominant males being heavier and obtaining a greater proportion of matings than subordinates (Herrera and Macdonald, 1993). There is no evidence of dominance relations among females. Groups occupy relatively small home ranges (ca. 10 ha) that are defended against intruders and, therefore, can be considered territories (Herrera and Macdonald, 1989). In the llanos, capybaras can breed throughout the year, but there is a peak in sexual activity in the early wet season (May—Herrera and Macdonald, 1993). We describe patterns of scent marking in capybaras in relation to their social system, with special reference to the males' dominance hierarchy. Having described the context of scent marking in free-living social groups of capybaras, we thereby draw inferences about the function of these behavior patterns. We also test the hypothesis proposed by Macdonald et al. (1984) that the size of a male's morrillo is an indicator of social status.

#### STUDY AREA AND METHODS

Capybaras were observed between March and October 1982–1984 around scattered, shallow pools on a ranch named Hato El Frio (7°46'N, 68°57'W) in the Venezuelan low llanos (state of Apure). Flat tropical savannas are flooded between May and October and endure drought in February and March, when capybaras suffer high, density-independent mortality (Ojasti, 1978). The observation period spanned the time when groups coalesce at the end of the dry season and then redefine themselves at the start of the wet season. It includes the mating period and the months when the females are pregnant.

Individuals were captured each February either by lassoing them from horseback or using a "dog-catcher noose" or catchpole to "fish" them up from thorny thickets of *Cassia aculeata*. Length of hind foot was measured, and weight was estimated from a measure of girth (Herrera, 1986). Length and height of the morrillo of males also were measured. Individuals were marked with expanding plastic collars (similar to those used by Clutton-Brock et al., 1982) and painted with unique two-letter codes (details in Herrera, 1986).

Groups were selected for intensive study on

the basis of accessibility and numbers of marked animals and observed in turn during sessions  $\leq 12$  h. Observations were evenly spread throughout the daylight hours for each group. Episodes of scent marking were scored as events (Altmann, 1974; Martin and Bateson, 1986) and recorded as they occurred, along with time and individual identity. States such as grazing, resting, and wallowing were recorded during scans of the group every 10 min (Altmann, 1974). The rates at which individuals performed event-type behavior were dependent on the amount of time each animal was in sight, which varied among animals (Herrera and Macdonald, 1987). To account for this variation in durations of observations, the proportion of time each animal was present during observation sessions, calculated from scan data, was used as a correction factor for behavioral rates.

#### RESULTS

Scent marking was the most common event performed by capybaras. In 729 h of observation over three field seasons, scent marking was observed a total of 3,864 times (1,115 morrillo and 2,749 anal gland) or 5.3 marks/h of observation. Anal glands were used in 71.4% of all scent-marking episodes, and 27.1% of them occurred just after a morrillo mark by the same individual on the same plant.

Adult males scent marked significantly more often per capita than adult females:  $\bar{X}$  (males) =  $1.51 \pm 0.93$  (SE) marks/h/individual while  $\bar{X}$  (females) =  $0.39 \pm 0.25$  (both glands pooled, Mann-Whitney test:  $n$  (females) =  $n$  (males) = 15;  $W = 134.0$ ,  $P < 0.001$ ). Among males, 68.2% of 782 morrillo marks were followed by anal gland marks, whereas, among females, 66.8% of 190 morrillo marks were followed by anal-gland marks; these proportions did not differ significantly between males and females ( $\chi^2 = 0.12$ ,  $d.f. = 1$ ,  $P > 0.05$ ). However, marks with anal glands were more frequently followed by morrillo marks by males (29.5% of 1,805 anal-gland marks) than by females (20.3% of 626:  $\chi^2 = 20.07$ ,  $d.f. = 1$ ,  $P < 0.005$ ). In other words, females tended to mark with only their anal gland

more often than did males. Total rate of group-marking decreased with group size ( $r_s = -0.465$ ,  $n = 14$ ,  $P < 0.05$ ) as a result of an even greater trend for diminishing individual marking rates with group size ( $r_s = -0.719$ ,  $n = 14$ ,  $P < 0.01$ ).

Sometimes an individual marked a particular plant just after another animal had marked it. It was difficult to record this systematically, but, of 56 occasions when this was seen, a female marked over the mark of a dominant male in 17, and a female marked over the mark of a subordinate male in only five instances. A subordinate male marked over a dominant's mark twice, whereas a dominant male marked over a subordinate's mark six times. Suitable plants for marking were scarce, and most were marked by many individuals of the same group on any 1 day.

During a total of 25.6 h of observations of one well-known group, we noted whether the animal sniffed at the plant before marking, the number of strokes given with the morrillo, and the height on the plant at which the scent was deposited (using an ordinal 1-to-3 scale relative to the height of the head of the animal). From these observations, we found that subordinate males were significantly more likely to sniff at a plant before marking it (34.2% of occasions) than were dominant males (18.4%:  $\chi^2 = 7.27$ ,  $d.f. = 1$ ,  $P < 0.01$ ). However, there was no significant difference in the per capita number of strokes per morrillo mark between dominant males ( $\bar{X} = 11.21 \pm 9.17$ ) and subordinates ( $\bar{X} = 9.13 \pm 5.45$ ; Mann-Whitney test:  $n$  (dominants) =  $n$  (subdominants) = 38;  $W = 1,495.0$ ,  $P = 0.754$ ). There also was no significant difference between dominant and subordinate males with respect to the height at which the scent was deposited (Mann-Whitney test,  $P > 0.05$ ).

There was a significant correlation between marking rate and rank in the hierarchy for both glands ( $r_s = -0.369$ ,  $n = 53$ ,  $P < 0.01$ ) and each gland taken separately (anal gland:  $r_s = -0.358$ ,  $n = 53$ ,  $P < 0.01$ ;

morrillo,  $r_s = -0.321$ ,  $n = 53$ ,  $P < 0.02$ ). Also, as a group, dominant males marked significantly more often than subordinates did (both glands, Mann-Whitney:  $n$  (dominants) = 15,  $n$  (subdominants) = 38;  $W = 509.0$ ,  $P < 0.05$ ). This also was true for the morrillo only, but not for the anal gland.

Context was defined as the animal's event-type behavior during the 2 min before scent marking. The most common context was scent marking because animals frequently deposited several marks in succession. Excluding these, the most common context (255 of 291 or 87.6% of instances where the animal had previously done something other than marking) was aggression, with the aggressor marking more frequently than the recipient (72% of 255 cases;  $\chi^2 = 7.41$ ,  $d.f. = 1$ ,  $P < 0.01$ ). However, most scent marks were deposited out of any detectable event-type context (63.3%), and most aggressive interactions involved no scent marking (only 12% of 2,084 aggressive interactions). Other contexts included 'sexual pursuit' and 'sniff another individual' but occurred at low frequencies. Only 21 times in 3 years did we record an animal marking on another animal, mostly (13 times) females on males and always with the morrillo.

The volume of the morrillo was estimated by the formula:  $V = \frac{1}{2}(h \times l^2)$ , where  $h$  is the height and  $l$  is the length of the gland. The volume of the morrillo correlated significantly with the dominance rank of males ( $r_s = -0.373$ ,  $n = 37$ ,  $P < 0.05$ ). As a group, dominant males had larger morrillos than did subordinates, although the difference was not statistically significant ( $\bar{X}$  (dominants) =  $31.73 \pm 9.27$  cm<sup>3</sup>,  $n = 11$ ;  $\bar{X}$  (subordinates) =  $23.53 \pm 12.50$  cm<sup>3</sup>,  $n = 26$ ; analysis of variance,  $F = 3.82$ ,  $d.f. = 1,35$ ;  $P < 0.10$ ). When correcting for body weight, neither the correlation coefficient between morrillo volume and rank nor the difference in morrillo volume between dominants and subordinates was significant, although both trends were the same.

## DISCUSSION

Scent marking was the most common type of social interaction among capybaras. Although capybaras do use vocalizations (alarm calls, a distress call, and a guttural purr, possibly a contact call given mostly by juveniles—Azcarate, 1980), chemical communication may be especially effective in an animal that is active during much of the night (Herrera, 1986; Macdonald, 1981).

Larger groups had lower scent-marking rates than did smaller groups, not only as a unit, but also individually. Since larger groups defended larger territories (Herrera and Macdonald, 1989), we infer that the home ranges of large groups are less thoroughly covered with scent than those of smaller groups. Male members of large groups are likely to be more loosely associated with their social units (Herrera and Macdonald, 1987) than those in smaller groups, and this difference in cohesiveness of membership may underlie the reduced marking activity of members of large groups. Similarly, larger groups have more subordinates, of ever-lower status, than do smaller groups, whereas the number of dominant males remains one irrespective of group size. Because subordinates mark less than dominants, the result will be that the average rate of marking falls with increasing group size.

Scent marking was much more common in males than in females. Males have many more aggressive interactions than do females (Herrera and Macdonald, 1993), and scent marking may function to indicate dominance, as in several other mammalian species (Huck and Banks, 1982; Novotny et al., 1990; Rylands, 1990; Ryon and Brown, 1990), but not in all cases (Holmes, 1990). Females also often mark just after the dominant male on the same plant, possibly indicating their association with him but possibly also to make sure that they are recognized as group members, since group

territorial defense involves males and females in both defender and intruder roles.

The relation between scent marking and social status among males is further emphasized by the differences in marking rates (and morrillo volume) between dominant and subordinate males, and by the greater length of time for which subordinates sniff at plants preparatory to marking them. The differences associated with status are most notable for the morrillo, concerning both the scent-marking rates and the size of the gland, so this gland may be especially important in this context. Herrera (1992) found a correlation between size of testes and size of morrillo (independent of body mass), suggesting a hormonal effect on morrillo development. A relation between hormonal status and rank has been found in cavies, capybaras' closest relatives (Sachser, 1988; Sachser and Prove, 1986), and also between size of scent gland and social status in other rodents (Barnett et al., 1980; Bronson and Marsden, 1973).

Because scent production also can be under hormonal control (Yahr and Cummins, 1983), a relationship between status, hormones, and scent production is likely; however, other functions of scent marking cannot be ruled out. One of the most frequently mentioned uses of scent marking by mammals is territorial demarcation (Gosling, 1990). Since capybaras defend territories, it is likely that scent marking functions for this purpose. However, unlike some other caviomorph rodents (e.g., Taber and Macdonald, 1984), capybaras do not drag either morrillo or anal pockets on the ground or on dirt mounds. They always deposit the secretion on a plant (or, in captivity, on fence poles). Thus, there are structural limitations to the locations of scent marks of capybaras. As they live on a grassland where the distribution of bushes and shrubs is patchy and irregular (Herrera and Macdonald, 1989), marks are necessarily similarly distributed. For this reason, the territory of a group of capybaras, although precisely limited in space (Herrera and



Macdonald, 1989), cannot be systematically marked on the borders. Perhaps the patterns of space utilization that are closely linked to activity patterns do not require capybaras to have an immediate deterrent at territorial borders. Capybaras have a regular daily routine of movements and also a regular routine of resting in mornings, and feeding in afternoons and evenings (Herrera and Macdonald, 1989; Macdonald, 1981). Territoriality in capybaras may be a mechanism for the maintenance of social cohesion as well as for the defense of limited resources (Herrera, 1986).

We cannot demonstrate whether scent marking by capybaras also functions in group membership identification, but the patterns of scent marking by females and subordinate males, especially for the anal gland, are compatible with this possibility. Females and subordinate males tend to use this gland more often singly (without the morrillo) than do dominant males. By depositing the anal-gland secretion on the territory, females and subordinate males may ensure that they are recognized as group members.

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