Chapter 10
Capybara Scent Glands and Scent-Marking Behavior

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10.1 Scent Marking in Mammals

Scent marking in mammals can convey a wide range of information (e.g., Brown 1979; Müller-Schwarze 1983; Brown and Macdonald 1985a, b; Arakawa et al. 2008), sometimes linked to agonistic behavior in ritualized contests over resources (e.g., Gosling 1990). Scent marks are used by some mammals to delineate territorial boundaries, as in Ethiopian wolves (Sillero-Zubiri and Macdonald 1998). They can also indicate group membership, as in matrilines of cats, *Felis sylvestris catus* (Passanisi and Macdonald 1990), individual identity, as in dwarf mongooses, *Helogale undulate* (Rasa 1973) or spotted hyenas, *Crocuta crocuta* (Drea et al. 2002) or social and sexual status as in giant otters, *Pteronura brasiliensis* (Leuchtenberger and Mourão 2008). 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). The latter is especially true in rodents, where status signaling appears to be the most common function of scent marking (Roberts 2007). Scent glands are commonly sexually dimorphic. Capybaras are unusual among caviomorph rodents in having not only anal glands but also a nasal gland, both of which are sexually dimorphic (Macdonald et al. 1984; Macdonald 1985).

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10.2 Morphology and Histology of the Scent Glands

10.2.1 Nasal Gland

Capybaras have a sexually dimorphic gland above the snout first described by Rewell (1949), which is very bulbous in the male but often barely visible in females (although some females have small-sized glands; Macdonald et al. 1984). This gland is known as the morrillo (after the Spanish morro, describing a small oblong hillock) and is an oval-shaped, shiny, blackish protuberance (Fig. 10.1). The morrillos of male capybaras are naked except for very sparse short hairs (*c*. 6.0 mm in length) and have a long axis of 6–7 cm and a width of 4–5 cm; they stand proud of the surrounding skin to a height of 1–3 cm (Macdonald et al. 1984). The oily surface glistens in the sun and is punctuated by distended pores out of which drops of creamy white, highly viscous secretion ooze (Macdonald et al. 1984). The size of the morrillo increases with age up to 25 months but thereafter any increase in size is not necessarily associated with age (Costa and Paula 2006). Larger, more dominant males have larger morrillos compared to subordinate males (Herrera and Macdonald 1994). Males with larger testes and higher levels of testosterone have larger morrillos (Herrera 1992; Costa and Paula 2006; López et al. 2008).

The morrillos are covered with a thick epidermal layer (*c*. 0.1–0.2 mm deep) beneath which the glandular layer is variously developed, averaging 8.2 mm (S.D. = 4.7, n = 44) in depth (Macdonald et al. 1984). The maximum depth of the glandular lozenge is different for males and females, at 10.5 mm (S.D. = 4.6, n = 25)

Fig. 10.1 Male capybara showing the morrillo, a thick scent gland on top of the snout (Photo by E.A. Herrera)

and 4.3 mm (S.D. = 1.1, n = 18), respectively, but for each sex the depth of glandular tissue increases with increasing body size class (Macdonald et al. 1984).

The glandular tissue is spongy in appearance, due to the presence of large lacunae or ampullae, measuring up to 1.5 mm in width and 6 mm in depth (Macdonald et al. 1984). The lacunae are filled with secretion and drain into pores leading directly to the surface. Around the hair follicles and the ampullae, there is ample evidence of secretory activity: disintegrating sebaceous cells and distorted nuclei border each lacuna and adjoin alveolar masses of sebaceous acini. One or several acini may drain into either a hair follicle or a lacuna leading directly to a pore. Connective tissue intrudes into the glandular mass, but less so for larger individuals of both sexes (Macdonald et al. 1984). Males have a greater area of sebaceous acini and lacunae per unit area than females and the larger males have more glandular tissue than smaller males, which takes the place of connective tissue (Macdonald et al. 1984).

10.2.2 Anal Glands

In both males and females, the anal glands are located beside and below the anus, lying within a chamber which contains the urogenital and anal pocket openings, all largely covered by the surrounding skin at rest (Macdonald et al. 1984). The morphology of the anal glands differs between males and females. In females, the anal pockets are relatively deep chambers which open through a constricted neck (depth 1.5 cm, chamber internal diameter 1.0–1.5 cm, neck *c*. 3 mm; Macdonald et al. 1984). Within the chamber the skin and hairs are coated with a smear of grayish, greasy material which when abundant may cause the hairs to be matted together (Macdonald et al. 1984). There is a large, solid mass of glandular tissue underlying the chamber (Macdonald et al. 1984).

The male anal pocket differs in being more an open pouch (approximately 4 × 3 cm) that can be easily pulled wide open and is not backed by the knot of tissue found in the glands of females (Macdonald et al. 1984). The pocket also contains hairs, but they are coated with a brittle gray-black deposit, giving them the shape of a club or truncheon (Fig. 10.2). The extent of the coating varies between hairs from a thin coating to a maximum cross-sectional diameter of 2.5 mm and length of 8.0 mm, with larger accumulations associated with longer (and therefore perhaps older) hairs (Macdonald et al. 1984). Hairs from a male's everted anal pocket are easily detached from the skin, and in general larger hairs are more easily detached than smaller ones (Macdonald et al. 1984). The hairs of the male anal pocket are narrower than the more bristle-like hairs of the female anal pocket, but both types are flimsier than body hairs such as those found on the back and inner thigh.

The tissues lining the anal pocket of males are highly glandular. They are, however, shallower and have less sebaceous cell development and sebaceous activity than female anal pockets (Macdonald et al. 1984). They are also different in tissue appearance, with ducts of sebaceous acini opening either into hair follicles or

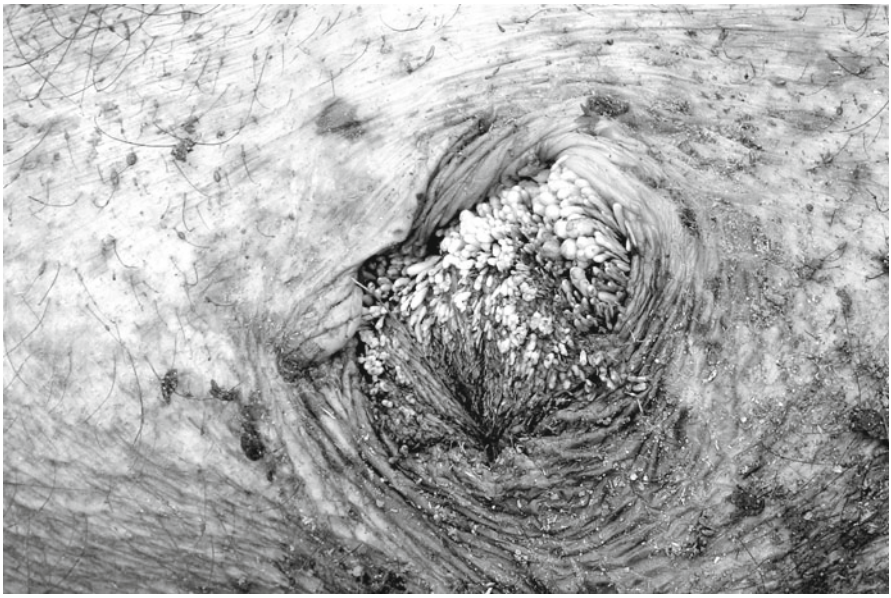

Fig. 10.2 Male anal pocket with hairs coated with a gray-black deposit in the shape of a club (Photo by J.R. Moreira)

directly through the epidermis along empty hair follicles (Macdonald et al. 1984). Within the gland, lacunae up to 2 mm in length and 0.25 mm in width are formed in the acini from cellular debris and secretions (Macdonald et al. 1984). Generally in males, larger individuals have more sebaceous cell development and sebaceous activity than do smaller individuals; however, a small sample of juvenile males had highly active, dense sebaceous tissue comparable to that of adult females (Macdonald et al. 1984). The hairs in the anal pocket of males are coated by an amorphous solid substance which in turn is encased by layers of crystalline material (up to *c*. 20 distinct layers; Macdonald et al. 1984). The annular structure is likely to arise from the drying of successive coatings of secretion, adhesion being aided by the overlapping scale pattern on the surface of the hairs (Macdonald et al. 1984). Bacteria from Streptococci group D, gram negatives, and Clostridia have been found within the hair coating, but it is not known whether these bacteria play a role in developing odors (as has been shown in other mammals; Albone et al. 1978; Lanyon et al. 2007) or were simply contaminants from the intestinal flora (Macdonald et al. 1984).

The swollen knot of tissue under the female anal pocket has highly dense, active sebaceous cells (Macdonald et al. 1984). While the largest size class of females has greater sebaceous cell development, there are no overall differences between size classes. The activity of sebaceous tissue is greater in larger females (Macdonald et al. 1984).

10.3 Chemical Composition of the Secretions

10.3.1 Nasal Gland

Secretions from the male nasal glands are a complex mixture of sterols and/or terpenes, lipids, and amino acids with up to 54 compounds found within a sample from a single individual (Macdonald et al. 1984). Lipids are the main component of the secretion, consisting of a mixture of esters of long chain fatty acids, and the most volatile substance found was a hydrocarbon, $C_{30}H_{50}$ (Macdonald et al. 1984). Each male had most of the compounds present but in significantly different proportions, possibly to aid individual recognition (Macdonald et al. 1984).

10.3.2 Male Anal Gland

The crystal deposits attached to the hairs within the male anal gland are principally composed of a calcium salt with some magnesium and trace amounts of silicon, phosphorous, aluminum, sulfur, and potassium (Macdonald et al. 1984).

10.3.3 Female Anal Gland

The greasy secretion from the female anal gland consists of sterols, terpenes, lipids, and amino acids, with up to 30 compounds found in the secretion from a single individual (Macdonald et al. 1984). The presence and amount of each compound varies between individuals, both in terms of relative and absolute concentrations (Macdonald et al. 1984).

10.4 Capybara Scent Marking Behavior

Scent marking in capybaras is much more common in males than females (Herrera and Macdonald 1994), but during courtship, males and females mark with equal frequency and use both glands (Schaller and Crawshaw 1981). A typical marking sequence for males involves rubbing the morrillo against a shrub or twig (Fig. 10.3), then straddling the plant, pressing the anal pocket onto it (Fig. 10.4) and, at least sometimes, simultaneously urinating on the plant (Azcaráte 1980; Macdonald 1985; Macdonald et al. 1984). During this process, hairs from the anal pocket are detached (Macdonald et al. 1984). Suitable plants for marking are often scarce within capybaras' habitat and so are marked by many individuals from the same group within any single day (Herrera and Macdonald 1994).

Fig. 10.3 Male capybara rubbing his nasal gland on a post (Photo by R. Barreto)

Fig. 10.4 Female capybara rubbing her anal glands on a twig (Photo by E.A. Herrera)

Dominant males have higher marking rates than do subordinate males for both types of gland, and subordinate males are more likely to sniff at a plant before marking it (Herrera and Macdonald 1994). The differences associated with status are most notable for the morrillo, for both scent-marking rates and the size of the gland (Herrera and Macdonald 1994). Marking occurs commonly without any social provocation, but will sometimes follow aggression, in which case the victor or both parties carry out marking, but it is rare for the vanquished male alone to do this (Herrera and Macdonald 1994). It is also very frequent during courtship, where the male overmarks, in particular, female anal marks. On rare occasions, males rub with their morrillos on the necks of females or subordinate males (Macdonald 1985) or females rub their morrillos on the necks of males (Herrera and Macdonald 1994). Males often sniff at the rear of females, particularly during courtship as they herd the female toward water to mate (Macdonald et al. 1984).

The morrillo and anal glands may also be used in separate scent-marking patterns, and females more often tend to mark only with their anal glands than do males; subordinate males do this more commonly than dominant males (Herrera and Macdonald 1994).

Larger groups have lower scent-marking rates than smaller groups, both as a unit and individually (Herrera and Macdonald 1994). Since larger groups defend larger territories (Herrera and Macdonald 1989), it is likely that the home ranges of large groups are less thoroughly covered with scent than those of smaller groups.

10.5 Capybara Scent Gland Marking: Possible Functions

Scent marking is the most common type of social interaction among capybaras (Herrera and Macdonald 1994). Although capybaras do use vocalizations (Azcaráte 1980), chemical communication may be especially effective in an animal that is active during much of the night (Macdonald 1981; Herrera 1986). The differences between individuals in the chemical composition of secretions may facilitate individual recognition from the scent marks (Macdonald et al. 1984; Macdonald 1985; Roberts 2007). One of the main functions of scent marking (particularly using the morrillo) in capybaras is thought to be the maintenance of the strict social hierarchy in males (Herrera and Macdonald 1993; Salas 1999), due to different scent-marking behavior in males of lower status, as outlined above (Herrera and Macdonald 1994). This is consistent with the general pattern observed among rodents (Roberts 2007). In capybaras, since the dominance hierarchy, and especially the dominant position, are maintained year-round and for several years (Herrera and Macdonald 1993), the role of scent marking in the maintenance of social status cannot be overestimated. This is further corroborated and emphasized by the large investment in testosterone-producing tissue at the expense of sperm-producing tissue in testes of capybaras (Moreira et al. 1997; Costa and Paula 2006; see also López et al. 2008; Paula and Walker 2012), leading to a correlation between testosterone concentration in blood and size of the

morrillo (Costa and Paula 2006). Moreira et al. (1997) have also suggested that the morrillo may be a visual signal of dominance.

Scent marking is also commonly used in mammals to demarcate territory (Gosling 1990); as capybaras defend territory it is possible that scent marking is also used for this purpose (Herrera and Macdonald 1994). However, as the secretion is always deposited on a plant, there are structural limitations to the locations of scent marks of capybaras. The distribution of bushes and shrubs in capybaras' habitat is patchy and irregular (Herrera and Macdonald 1989) and, therefore, so are the scent marks. 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. As the patterns of space utilization are probably closely linked to activity patterns, it is possible that capybaras do not require an immediate deterrent at territorial borders (Herrera and Macdonald 1994), but marking of territory may provide a mechanism for social cohesion as well as for the defense of limited resources.

It is possible that scent marking also functions in identification of group membership, particularly in the patterns shown by females and subordinate males using the anal gland (Herrera and Macdonald 1994). Females often mark just after the dominant male, possibly to indicate their association with him as well as possibly to demonstrate their group membership (Herrera and Macdonald 1994).

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