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Mammalian Scent Gland Marking and Social Behavior

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Scent-marking behavior is a common method of olfactory communication among mammalian species. Here we review concepts of scent marking and present naturalistic and laboratory illustrations of intraspecific communication. The most informative data and comparative possibilities exist for the following species: ground squirrel, Mongolian gerbil, golden hamster, guinea pig, pika, sugar glider, European rabbit, pronghorn antelope, blacktail deer, Maxwell duiker, lemur monkey, and marmoset monkey. The review points out generalities and differences among these species and hopefully indicates how behaviorists and other biologists, with their unique laboratory and measurement skills, can contribute to the advancement of this research.

Information on mammalian scent marking is accumulating at a rapid pace (Birch, 1974; Cheal & Sprott, 1971; Eisenberg & Kleiman, 1972; Ewer, 1968; Gleason & Reynierse, 1969; Johnson, 1973; Johnston, Moulton, & Turk, 1970; Mykytowycz, 1970; Ralls, 1971; Sebeok, 1968). It is becoming increasingly evident that a large share of mammalian social behavior centers around the active deposition of organic chemicals, chemicals that integrate individual and population behaviors and specify which genetic complexes are transmitted to subsequent generations. Behaviorists in general and zoologists in particular are researching these problems. It is hoped that this review will focus greater attention on scent-marking behavior and stimulate increased concern by psychologists as well as other biologists. The review summarizes concepts revolving around chemical communication, suggests criteria for defining scent-marking functions, and describes the findings for those mammalian species that have received detailed attention. Finally, commonalities and differences between species are discussed and an attempt made to suggest evolutionary precursors of scent-marking behavior.

CONCEPTS OF CHEMICAL COMMUNICATION

A great deal of social behavior is dependent on an intact olfactory system (Alberts & Friedman, 1972; Bandler & Chi, 1972; Devor & Murphy, 1973; Edwards, Thompson, & Burge, 1972; Ropartz, 1968; Rowe & Edwards, 1971). In fact, the growing recognition of the importance of olfactory communication led André Steiner at the University of Alberta (Note 1) to remark that the dominant mode of mammalian signaling is olfactory. Certainly there is overwhelming evidence that chemical signals of an olfactory nature modify many social activities of mammals. Mykytowycz (1970) suggested that mammalian chemosignals can have the following functions:

Intraspecific communication

Individual and group recognition
Age, sex, and reproductive status recognition

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Home range, territory, and trail identification
Warning, defense, and alarm
Distress and pain signaling
Social dominance or submissiveness identification

Interspecific communication

Individual and species recognition
Prey or predator signaling
Warning and defense signaling

The multiple functions given by Mykytowycz (1970) for intraspecific communication, the concern of this review, revolve around three major classes of signals: those used for (a) aggregation, (b) recognition, and (c) population control. Ultimately, each class has a bearing on the constitution of the gene pool, as indicated in Table 1. In one way or another, a chemosignal has an influence on individual and species survival, thus it can be assigned a value related to genetic fitness. Viewed in this way, chemicals convey social *and* genetic messages.

Functionally, chemical signals are capable of transmitting every bit as much information as visual, auditory, or tactual cues. They vary in intensity and time, and through molecular gradients specify direction and distance (Wilson, 1968). They possess patterns or medleys, synergize in multiple ways, and take on meaning according to early experiences and environmental context. And, like visual and auditory stimuli, chemical signals can relay information concerning physiological and behavioral states (Bronson, 1971, 1974). The myth that chemosignals are primitive, affecting only rudimentary processes, has largely been exploded because sophisticated research strategies have exposed their complexities.

Traditionally chemical signals have been termed *ectohormones,* after Bethe (1932), and more recently *pheromones,* after Karlson and Butenandt (1959), who, after prodigious efforts, obtained a female moth sex attractant (bombykol) from the extract of 250,000 female moths. Although criticism has abounded on the use of the term *pheromone,* it has been solidly established in the literature. The word is derived from the Greek *pherein* meaning to carry, and *horman* meaning to excite.

The classic work with insects has perpetuated the definition of a pheromone as a chemical released to the outside of the body affecting the physiology and behavior of another individual. Based again on the insect model, several criteria must be satisfied before a released chemical can be technically termed a pheromone. It must be a single compound and have a specific source of origin, usually a gland. It must be detected by a specialized receptor system (e.g., the olfactory sensor cells). The chemical must be species specific, at least among sympatric species (chemical signals used for communication *between* species are termed *allomones,* after Brown, 1968). It must convey a message that is

TABLE 1

INTEGRATIVE FUNCTIONS OF SCENT GLANDS AND OLFACTORY COMMUNICATION

Signal	Significance for the gene pool
Aggregation	Signals may have directional qualities, bringing conspecifics together so that territories or dominance orders can be established and differential mating occur. Aggregation is primary to any other function.
Recognition	In restricted gene pools, it is essential that social and physiological distinctions can be made with ease. Animals must be able to discriminate individuals, group and species memberships, age, sex, social status among peers, and reproductive and aggressive status of other males and females.
Territorial defense, social status, and dispersal	Territories or social status are assumed and defended for multiple reasons. These behaviors personalize situations, provide food, shelter and mates, disperse population members, encourage migration, reduce overt aggression and the spread of disease and parasites, decrease predation, increase inbreeding, and maintain reproductive potential among nonbreeding subordinates.

clearly understood by the recipient and affect reproductive fitness. Finally, it is also presumed by some investigators that the pheromone should evoke a discrete stereotyped response. It is unusual for a pheromone to satisfy all these criteria. In fact, most mammalian chemosignals fail to meet one or more criteria, yet in a general sense can still be considered to be pheromones. This is true as long as the signals originate from metabolic processes, satisfy physical transmission characteristics, and convey information. Whether they are imprinted on the receiver, genetically invariant, or situational specific makes little difference in terms of adaptive functions.

Pheromones can be gustatory or cutaneous, as well as olfactory, but by far the greatest research interest has centered around olfactory stimuli. A noteworthy exception is the identification of a queen bee substance, 9-oxodec-2-enoic acid, excreted by the mandibular gland of the queen. When ingested, this substance retards the sexual development of female workers (Butler, Callow, & Johnston, 1961). It also inhibits queen cell construction and, as an olfactory molecule, stimulates nuptial flight (Gary, 1974). With recent advances in laboratory techniques and in the short space of a few years, many dozens of insect pheromones have been characterized (Blum, 1974; Butler, 1970). They act as alarm and alerting stimuli, as trail markers, aphrodisiacs, territorial and aggregation stimuli, and even as regulators of development and sexual differentiation. Almost all of these are airborne and have relatively low carbon numbers and molecular weights (between 5 and 20 carbons and molecular weights within 80 to 300, Wilson and Bossert, 1963). Intermediate carbon numbers and low molecular weights allow for chemical diversity and high volatility.

Pheromones are also classified according to their mode of activity, specifically as *releasers, primers,* or *signals.* A releaser pheromone is one which triggers a neurologically programmed response immediately upon stimulation. A primer pheromone changes the physiology of an organism, usually over a long period of time, and predisposes the organism to respond in certain ways. Both a releaser and a primer depend heavily upon the genetic programming of the species. A signal pheromone, on the other hand, is a substance that conveys information but does not necessarily evoke a response. It can have strict genetic programming or depend heavily on learning. Moreover, signaling pheromones may also act as primers. In specific cases it is sometimes difficult to differentiate the three.

CHEMICAL COMMUNICATION THROUGH SCENT GLANDS

The widespread use of chemical communication is suggested by the frequent appearance of scent glands in many species. According to Müller-Schwarze (1967), scent glands have been described in 15 of the 19 mammalian orders, and on the basis of location on the body, as many as 40 different types can be classified. One species may possess a varied assortment of glands. Lagomorphs, for example, have chin glands, anal glands, paired inguinal glands, and Harder's infraorbital and lachrymal glands situated in the orbit (Mykytowycz, 1965, 1966a, 1966c, 1970). The flying phalanger possesses a major frontal gland and smaller glandular areas near the ears and at the angle of the eye (Schultze-Westrum, 1965). Arctic and Columbian ground squirrels have scent glands at the corners of the mouth, in the anal area, and on the dorsal surface (Steiner, 1974). Mongolian gerbils have a midventral scent pad and secretory tissue under the chin and neck area (Thiessen, 1973).

Secretory cells, often constituting the scent glands used in chemical communication, are of two types: holocrine, as in the ventral gland of the Mongolian gerbil, and apocrine, as in the chin gland of the European rabbit. Holocrine glands form sebum from the total breakdown of sebaceous cells. On the other hand, apocrine glands synthesize sebum without cellular disintegration and pass the sebum out of the cell.

Apocrine and holocrine glands may appear in different species but are suspected of performing similar behaviors. For instance, apocrine glands appear in the chin complex of the rabbit (*Oryctolagus cuniculus*) and hare (Leporidae) and cheeks of the cottontail (*Sylvilagus floridanus*), whereas holocrine glands

TABLE 2

REPRESENTATIVE MAMMALIAN SPECIES WITH SPECIALIZED SCENT GLANDS AND BEHAVIORAL MARKING

Order	Family	Genus	Species	Common name	Distribution	Gland characteristics	Behavioral characteristics and social implications	References
Artiodactyla (ungulates)	Bovidae	*Antilope*	*cervicapra*	Blackbuck	South Asia	Preorbital gland	Objects marked with preorbital secretion.	Hediger (1949), Tembrock (1968)
	Cervidae	*Capreolus*	*capreolus*	Roe deer	Europe and Asia	Forehead gland	Marks branches at territorial boundaries.	Prior (1968)
	Bovidae	*Cephalophus*	*maxwelli*	Maxwell duiker	Central West Africa	Preorbital gland	Objects and conspecifics marked, especially by dominant male. Individuals press glands together. Males mark more frequently, and both sexes mark more frequently in presence of same sex.	Ralls (1971)
	Bovidae	*Rupicapra*	*rupicapra*	Chamois	Europe and Asia	Occipital gland	Social interaction stimulates marking. Dominant animals mark more frequently than subordinate animals.	Kramer (1970)
	Tayassuidae	*Tayassu*	*tajacu*	Collared peccary	South and Central America	Lumbar glandular area	Bends hind legs and rubs gland on grass, tree stumps, and other objects, depositing milky secretion.	Fradrich (1967)
	Cervidae	*Odocoileus*	*hemionus*	Mule deer (black-tailed deer)	West and North America	Preorbital gland, tarsal gland, metatarsal gland, interdigital glands	Preorbital gland used to mark objects. Tarsal gland used in aggressive displays by dominant males, and in males and females for individual and sex recognition.	Brownlee, Silverstein, Müller-Schwarze, & Singer (1969), Müller-Schwarze (1967, 1969a, 1969b, 1971), Müller-Schwarze & Müller-Schwarze (1969)
	Antilocapridae	*Antilocapra*	*americana*	Pronghorn antelope	North America	Subauricular gland	Gland used to mark bushes and grasses, especially around borders of territories.	Moy (1970), Müller-Schwarze (1974)
Carnivora (carnivores)	Canidae	*Nyctereutes*	*procyonoides*	Racoon dog	East Asia and Sourh America	Glands at dorsal root of tail	Glands rubbed on roof of lair.	Ewer (1968)
	Canidae	*Vulpes*	*vulpes*	Red fox	North America, Asia, North Africa and Europe	Glands at dorsal root of tail	Glands rubbed on entrance of refuge.	Ewer (1968)
	Viverridae	*Cryptoprocta*	*ferox*	Fossa	Madagascar	Chest gland	Gland larger in males, although both males and females mark substratum. Glands maximally active during breeding season.	Ewer (1968), Vosseler (1929)
	Viverridae	*Helogale*	*undulata*	Dwarf mongoose	East Africa	Facial glands	Marks substratum with chest glands.	Ewer (1968), Tembrock (1968), Zannier (1965)
	Viverridae	*Herpestes*	*edwardsi*	Indian grey mongoose	South Asia	Facial glands	Marks objects with cheek glands.	Dücker (1965), Ewer (1968)
Edentata (edentates)	Bradypodidae	*Bradypus*	*tridactylus*	Three-toed sloth	South America	Middorsal skin gland	Back rubbed against substrate.	Tembrock (1968)
Lagomorpha (rabbits and hares)	Leporidae	*Oryctolagus*	*cuniculus*	European rabbit	Europe and North America	Apocrine chin gland, anal gland	Marking generally done by dominant male. Gland and marking more prominent in male and are androgen dependent.	Myers & Poole (1961), Mykytowycz (1965, 1968), Wales & Ebling (1971)

TABLE 2—*Continued*

Order	Family	Genus	Species	Common name	Distribution	Gland characteristics	Behavioral characteristics and social implications	References
	Leporidae	*Sylvilagus*	*aquaticus*	Swamp rabbit	North America	Chin gland	Marking generally done by dominant male and in the presence of a female, another male, or in isolation. Underside of chin rubbed on objects.	Marsden & Holler (1964)
	Leporidae	*Sylvilagus*	*floridanus*	Cottontail rabbit	North America	Chin gland	Similar to swamp rabbit, but marking less frequent.	Marsden & Holler (1964)
	Ochotonidae	*Ochotona*	*princeps*	American pika	North America	Cheek gland	Gland rubber on twigs and other objects.	Barash (1973), Harvey & Rosenberg (1960)
Marsupialia (marsupials)	Dasyuridae	*Antechinus*	*flavipes*	Yellow-footed marsupial mouse	Australia	Sternal glands	Chest rubbing on branches. Glands and behavior especially evident in males.	Ewer (1968)
	Phalangeridae	*Petaurus*	*breviceps*	Short-headed flying phalanger (sugar glider)	Australia and New Guinea	Frontal glands and sternal glands	Marking of self, mate, and territory, especially by dominant male. Odors of individuals and groups can be distinguished.	Ewer (1968), Schaffer (1940), Schultze-Westrum (1965, 1969), Tembrock (1968)
	Phalangeridae	*Phascolarctus*	*cinereus*	Koala	Australia	Sternal gland	Marking more often in male than in female.	Ewer (1968)
	Phalangeridae	*Trichosurus*	*vulpecula*	Brush-tailed phalanger	Australia	Sternal glands	Chest marking of branches most common	Ewer (1968)
Primates (monkeys and apes)	Cebidae	*Ateles*	*geoffroyi*	Central American spider monkey	Central and South America	Apocrine glands on sternal, gular, and epigastric areas	Chest marking of objects.	Eisenberg & Kuehn (1966), Epple & Lorenz (1967)
	Hapalidae	*Micro*	*argentatus*	Silvery marmoset	South America	Sebaceous glands on sternal and gular areas	See comments for *Callimico goeldii*.	Epple (1967)
	Indridae	*Propithecus*	*verreauxi*	Verreauxi's sifaka	Madagascar	Long scent gland on ventral surface of throat	Throat marking most frequent where females urinate and during intertroop encounters.	Jolly (1966), Petter (1962a, 1962b)
	Lemuridae	*Hapalemur*	*griseus*	Grey gentle lemur	Madagascar	Brachial gland	Marking has been reported.	Andrew (1964)
	Lemuridae	*Lemur*	*catta*	Ring-tailed lemur	Madagascar	Sebaceous brachial gland on upper chest near arm pit; apocrine and accrine glands on forearm	Complex fighting display in which glands are used to anoint the body, especially the tail which is waved at other animals.	Jolly (1966), Petter (1965), Petter-Rousseaux (1964)
	Lemuridae	*Lemur*	*macaco*	Black lemur	Madagascar	Sebaceous glands in anogenital region	Males mark females and objects. Dominant males will mark subordinate males.	Jolly (1966), Petter (1962a, 1962b, 1965)
	Lorisidae	*Loris*	*tardigradus*	Slender loris	South Asia	Apocrine brachial gland	Marking known but not described in detail.	Hill (1956a, 1956b)
	Tupaiidae	*Tupaia*	*glis*	Common tree shrew	South Asia, Sumatra, Java, Borneo	Apocrine glands from chin onto sternum; larger in male	Regular marking areas. Marking and gland more pronounced in dominant male, especially during aggressive encounters.	Andrew (1964), Kaufmann (1965), Sprankel (1961)
	Cebidae	*Callicebus*	*moloch*	Orabussu titi	South America	Apocrine glands on sternal, gular, and epigastric areas	Chest marking of branches and hands, especially in intergroup encounters.	Mason (1966), Moynihan (1966)
	Cebidae	*Lagothrix*	*cana*	Smoky woolly monkey	South America	Apocrine glands on sternal, gular, and epigastric areas	Chest marking of objects.	Epple & Lorenz (1967)

(table continued)

TABLE 2—*Continued*

Order	Family	Genus	Species	Common name	Distribution	Gland characteristics	Behavioral characteristics and social implications	References
	Cebidae	*Lagothrix*	*logothricha*	Humboldt's woolly monkey	South America	Apocrine glands on sternal, gular, and epigastric areas	Regular marking areas. Chest marks objects.	Epple & Lorenz (1967)
	Cebidae	*Saimiri*	*sciureus*	Common squirrel monkey	South America	Apocrine glands on sternal, gular, and epigastric areas	Regular marking areas.	Epple & Lorenz (1967)
	Cebidae	*Callimico*	*goeldii*	Goeldi's monkey	South America	Sebaceous glands on sternal and gular areas	Regular marking areas. For most Cebidae, marking glands mature at puberty; marking is done mostly by dominant male and is directed toward objects or conspecifics.	Epple & Lorenz (1967)
	Callithricidae	*Callithrix*	*jacchus*	Common marmoset	South America	Sebaceous glands on sternal and gular areas	Marking in dominant male increases after fighting encounters but not in female. Objects marked by other Callithricidae stimulate marking.	Epple (1967), Epple & Lorenz (1967)
	Callithricidae	*Callithrix*	*leucophala*	White-footed marmoset	South America	Sebaceous glands on sternal and gular areas	See comments for *Callimico goeldii.*	Epple (1967)
	Callithricidae	*Leontideus*	*rosalia*	Golden lion marmoset	South America	Sebaceous glands on sternal and gular areas	Regular marking areas. (See comments for *Callimico goeldii*).	Epple & Lorenz (1967)
Proboscidae (elephants)	Elephantidae	*Loxodonta*	*africana*	African Elephant	Africa	Apocrine temporal gland	Scent delivered to conspecific by trunk. Gland most active during rut.	Kuhme (1961), Tembrock (1968)
Rodentia (rodents)	Cricetidae	*Arvicola*	*terrestris*	Water vole	Europe and Asia	Flank glands	Marking accomplished by rapid wiping of flanks by hind feet, followed by foot-stomping.	Brown (1966), Frank (1956)
	Cricetidae	*Meriones*	*hurrianae*	Gerbil	North Africa and Asia	Ventral scent gland	Ventrum rubbed on surfaces. Response often associated with "sandbathing" movements.	Eisenberg (1967)
	Cricetidae	*Meriones*	*unguiculatus*	Mongolian gerbil	Northeast Asia	Sebaceous ventral gland and gular sebaceous gland	Marking generally by ventral gland, especially in dominant males. Gland and marking more prominent in male, and are androgen dependent in male. Defeated males avoid smell of dominant animals.	Eisenberg (1967), Nyby, Thiessen, & Wallace (1970), Thiessen (1968)
	Cricetidae	*Meriones*	*tristrami*	Gerbil	North Africa	Sebaceous ventral gland	Marking by ventral gland especially in males. Gland and marking are androgen dependent.	Thiessen, Wallace, & Yahr (1973)
	Cricetidae	*Mesocricetus*	*auratus*	Golden hamster	East Europe and West Asia	Sebaceous gland on flanks	Regular marking areas. Marking prominent around diestrous females or other hamster smells. Male will mark defeated rival who in turn will subsequently avoid smell of dominant animal. Gland and marking appear at puberty and are androgen dependent. Marking more frequent in male, but both sexes mark more frequently in presence of same sex.	Dieterlen (1959), Eibl-Eibesfeldt (1953a, 1953b, 1953c, 1953d), Ewer (1968), Johnston (in press-a) Murphy (1970, Note 3)

TABLE 2—(*Continued*)

Order	Family	Genus	Species	Common name	Distribution	Gland characteristics	Behavioral characteristics and social implications	References
	Cricetidae	*Neotoma*	*cinerea*	Wood rat	North and Central America	Ventral scent gland	Ventral marking of rocks, logs, etc., presumably for the purpose of defining territories.	Bailey (1936), Howell (1926), Linsdale & Levis (1951), Werner, Dalquest, & Roberts (1952)
	Heteromyidae	*Dipodomys*	*nitratoides*	Kangaroo rat	North America	Sebaceous dorsal gland	Regular marking area. Marking increases during exploration of novel area. Gland is apparently androgen specific. Ventral rub integrated with side-rubbing movements.	Eisenberg (1963, 1967), Quay (1953)
	Heteromyidae	*Heteromys*	*anomalas*	Spiny pocket mouse	Central and South America	Ventral scent gland	Ventrum rubbed on surfaces, usually in preferred areas. Not integrated with side-rubbing movements.	Eisenberg (1963, 1967)
	Heteromyidae	*Heteromys*	*iepturus*	Spiny pocket mouse	Central and South America	Ventral secnt gland	Ventrum rubbed on surfaces, usually in preferred areas. Not integrated with side-rubbing movements.	Eisenberg (1963, 1967)
	Heteromyidae	*Liomys*	*pictus*	Spiny pocket mouse	Central America	Ventral scent gland	Ventrum rubbed on surfaces, usually in preferred areas. Not integrated with side-rubbing movements.	Eisenberg (1963, 1967)
	Heteromyidae	*Perognathus*	*californicus*	Pocket mouse	North America	Sebaceous ventral gland	Regular marking area. Marking intense following exploration of novel area. Ventral rub integrated with side-rubbing movements.	Eisenberg (1963, 1967)
	Muridae	*Rattus*	*rattus*	Black rat	Europe, Asia, Australia, Africa	Sebaceous ventral gland	Regular marking area. Marking intense following exploration of novel area. Ventral rub integrated with side-rubbing movements.	Eisenberg (1963, 1967)
	Sciuroidea	*Citellus*	*beecheyi*	California ground squirrel	East Europe, Asia, North America	No apparent specialized gland area	Males and females mark objects by applying the entire ventral surface. Marking occurs especially during disturbances and entry of strange animals.	Ewer (1974), Linsdale (1946)
	Sciuroidea	*Spermophilus*	*columbianus*	Columbian ground squirrel	North America	Dorsal skin gland	Animals mark by turning over to press gland against object or by rubbing gland against overhang.	Kivett (1975), Steiner (1973)
	Sciuroidea	*Spermophilus*	*undulatus*	Arctic ground squirrel	North America	Dorsal skin gland and mouth gland	Animals exchange scents from mouth gland with a greeting kiss. They also mark the substrate with cheeks, throat, and belly. Males mark more often than females.	Steiner (1973)
	Sciuroidea	*Marmota*	*olympus*	Olympic marmot	Europe, Asia, North America	Dorsal skin gland and mouth gland	Animals exchange scents from mouth gland with a greeting kiss. They also mark the substrate with cheeks, throat, and belly. Males mark more often than females.	Barash (1973)

appear on the midventral surface and under the chin of the Mongolian gerbil (*Meriones unguiculatus*) and on the flank of the hamster (*Mesocricetus auratus*). On the other hand, the two general types may occur together, as in the inguinal glands of the rabbit or hare or the lateral glands of the short-tailed shrew (*Blarina brevicauda*). While not supported by evidence, Schaffer (1940) suggested that apocrine glands convey species-specific odors, whereas holocrine glands affect sexual behaviors. According to this speculation, a mixture of the two gland types would be most evident in reproductive processes related to individual recognition, aggregation, and courting behavior.

Table 2 lists those mammalian species that possess discrete scent glands and associated behaviors—behaviors presumably of social significance. Eight orders involving 55 species have these characteristics. Certainly, many more species will emerge that use scent glands for chemical communication, and even among those listed in Table 2, only the Columbian ground squirrel, European rabbit, sugar glider, blacktail deer, pronghorn antelope, Maxwell duiker, Mongolian gerbil, golden hamster, guinea pig, marmoset monkey, and lemur have been investigated to any great extent.

Many additional means of chemically marking the environment have evolved which are not indicated in Table 2. Anal rubbing or dragging is quite frequent, as are urination (including urine washing) and defecation. Less frequently used methods of marking include cloacal, cheek, and vaginal rubbing. Species displaying these responses do not have (a) the type of organized scent glands indicated for the species in Table 2, or (b) a mode of behavior clearly related to social interactions and chemocommunication. Once these species have been studied more thoroughly, it should not be surprising to find that most of the marking traits have social significance.

Marking objects, as well as conspecifics, with urine is a form of scent-marking behavior found in many species (Scott & Fuller, 1965). Although this type of scent marking is not the primary focus of this review, detailed information is available regarding behavioral components and situational influences, as well as some of the physiological control mechanisms involved in urine marking for several species, particularly the house mouse (Desjardins, Maruniak, & Bronson, 1973), the wolf (Peters & Mech, 1975), and the dog (Hart, 1974b). In fact, Hart (1974a) stated that the urination behavior of male dogs has characteristics typically associated with scent marking. Urine marking in dogs is sexually dimorphic, found only in males, and can often be separated from simply emptying the bladder. Two characteristics are associated with this behavior in males: the special leg-lift posture, which facilitates the application of urine on vertical objects, and the frequent deposition of urine on several objects over a short time (Hart, 1974a). A bout of urine marking can be triggered by a novel environment which includes the odors of other dogs. When the male dogs were placed singly into new pens, they urine marked a mean of 24.6 times during the first 2 hours and around 5 times in any other 2-hour sample over 7 days (Hart, 1974a). Marking was not accompanied by any sign of fear or aggression and may have been done primarily to permeate the environment with a familiar odor.

Urine marking may be reduced in males by neonatal castration and facilitated in females by perinatal androgen administration (Beach, 1974). This might imply that urine marking in the dog, as in many other species, is dependent on male sex hormones; however, Hart (1974a) found that 5 months after castration of male dogs, there was no change in either the latency to urine mark or the frequency of urine marks, even though in the same animals the frequency of sexual behavior was reduced within 2 months. The unusual period of hormone independence may be related to the animals' familiarity with the environment. In any case, the data imply that androgens have different effects on two sexually dimorphic behavior patterns in dogs, and further research is needed to clarify the role of androgen in urine marking in dogs and the relationship among this marking and other behaviors.

Desjardins et al. (1973) reported that in male house mice, both urination frequency and the pattern of deposition of urine in the environment depend on social rank. Using cages lined with filter paper and an ultraviolet light to detect the presence of urine, they found that when previously isolated males were paired across a wire barrier, both males deposited urine over the entire floor area. After these males were allowed to fight and establish a dominance relationship, only the dominant male continued to deposit urine throughout the environment, while the subordinate male concentrated all of his urine in one or two specific areas. Since the urine of adult mice has been thought to play a role in the enhancement and suppression of ovulation in immature and mature females and may even be able to prevent implantation in recently inseminated females (Parkes & Bruce, 1961), the dominant male's pattern of urine marking may give him a distinct fitness advantage over the subordinate males.

It is notable that many of the products used for marking are excrements of normal metabolic activities. Apparently, exudations often take on signaling capacities because they are present in large amounts as metabolic byproducts and can assume secondary functions as the result of natural selection. Similarly, reproductive variations result in a host of biochemical changes that can be selected for signaling capacities. For example, the body chemistry and sensitivity of olfactory perception of the female changes radically from the follicular to the luteal phase of the estrous cycle, leading to metabolic byproducts ideal for chemosignals (Pietras & Moulton, 1974). Likewise, the onset of puberty in both sexes and seasonal onset of breeding offer a wide array of chemical changes that could contribute to social signals.

Ultimately, several criteria must be met before it can be said that a scent gland has behavioral, evolutionary, and social significance. In ascending order of significance, it would seem that the following criteria must be established.

1. The gland should appear well organized and should interface with the substratum that the animal usually contacts. Thus, glands on the sides, flanks, and dorsal surfaces occur in a number of small rodents that either inhabit burrows or use runways through thick vegetation (Ewer, 1968). Among species that commonly sunbathe (e.g., Heteromyid) or depress their anal–genital area against the substrate because of any irritation (e.g., Carnivora and many rodents), anal gland smearing, vaginal rubbing, and cloaca rubbing are common (Gleason & Reynierse, 1969). In arboreal marsupials (e.g., koalas and phalangers) and New World primates (e.g., marmosets and tree shrews) that contact tree branches while climbing, sternal scent glands are often evident. Similarly, the passive marking of an environment during the course of other activities is associated with appropriately located scent glands. The interdigital glands of the mule deer (*Odocoileus hemionus*), for example, deposit a secretion on trails whenever the animal moves. This type of passive marking also occurs in species possessing pedal glands (e.g., Cervidae, Suidae, and possibly man).

2. For proficient use, a scent gland must be regulated in such a way that secretion is readily available and can be easily applied. This means that the sebum must be stored or rapidly synthesized. Moreover, the external ducts must provide openings to the environment that match the manner in which the substratum is approached. For example, the hairs protruding from the ventral gland of the Mongolian gerbil are grooved and orient toward the rear to allow the best possible deposition of sebum as the animal moves forward over an object.

3. Sexual dimorphism and seasonal variation should be evident in scent glands related to reproduction, implying that hormonal control is essential. Many of the species described in Table 2 show sexually dimorphic scent glands, with the male possessing the larger gland and usually the more frequent marking behavior. As expected, dimorphism of the glands at puberty, as in the European rabbit, ground squirrel, sugar glider, Mongolian gerbil, golden hamster, lemur monkey, and pronghorn antelope. Gland size is attenuated by castration and is exaggerated by the injection of sex hormones, as in the European rabbit, Mongolian gerbil, short-tailed shrew, dromedary, golden hamster, and guinea pig.

Likewise, seasonal variation is evident in the glandular activity of many species. Quay (1953) described variations in five species of

Dipodomys and stated that seasonal differences are apparent. The European rabbit (Mykytowycz, 1966a, 1966b, 1966c) and wood rat (*Neotoma fascipes*) (Linsdale & Levis, 1951), ground squirrel (Steiner, 1974), lemur monkey (Jolly, 1966), pika (Markham & Whicker, 1973), and pronghorn (Moy, 1970) all show scent gland activity that quickens during the breeding season. Apparently many scent glands and, presumably, related behaviors are most evident during life stages and seasons when sexual communication is necessary.

4. To be most effective, a scent gland should be stimulated by internal or external events most closely related to significant social behaviors. Evidence here is almost entirely lacking, with the obvious exception that the hormone status is critically important. In the female golden hamster, clitoral gland secretion follows examination of the lateral glands by the male (Lipkow, 1954). Nichol (Note 2) reported that male deer discharge scents when frightened or calling fawns. And, according to Mykytowycz (1970), musk glands discharge in fright situations in a wide variety of species (civets [Viverridae] and skunks [Mustellidae]).

5. A correspondence should exist within a species between the chemical nature of the scent gland secretion and the development of the receptor system. This criterion is one of the most difficult to establish. At the most basic level, it is expected that only macrosmatic animals would possess scent glands and that the olfactory material would be volatile and easily captured by the olfactory epithelium. We must also consider the possibility of intraspecific or interspecific communication in which one sex or species transmits a signal and the other receives the chemical message. In this case only the receiver need be macrosmatic. The successful isolation and identification of chemical signals may offer important clues to the understanding of complex neurological processes of olfaction. Once the stimulus is clearly defined, a detailed search can begin for olfactory receptors and electrophysiological changes in the central nervous system.

6. Scent glands should have exaggerated signaling qualities when other sensory systems are not used. Similarly, chemical communication will be enhanced when it is integrated with other modes of communication. Thus, it is expected that olfactory signaling will predominate in (a) nocturnal species, which cannot rely on visual displays; (b) species that live in thick foliage, in which visual displays are likely to be obscured; (c) terrestrial species whose vision or audition is obscured by terrain features; and (d) species with short home ranges, for which olfactory material can provide reliable signposts. Scent glands, in particular, may be used by desert species, which must conserve body water and hence cannot use desiccating responses such as urination, defecation, or salivation for object marking. In short, scent glands and marking must show ecological adaptiveness. No doubt some species use similar modes of signaling because of phylogenetic relations. But in other cases convergent evolution has driven diverse species toward a common method of communication. It is in the latter cases in which ecological adaptation takes precedence over common heritage.

Cercopithecodia species, such as the African and Asian baboons, macaques, guenons, mangabeys, langurs, colobus, and patas monkeys, which are swift arboreal, semi-terrestrial, and terrestrial species with large home ranges, do not have organized scent glands or marking patterns. Other primates (e.g., *Pithecia monocha, Cacajao rubicundus,* and *ateles*) often assume upright postures but have difficulty balancing. Apparently as a consequence, they have lost the capacity of scent marking (Moynihan, 1967). Man, of course, as an upright, highly mobile species relies mainly on vision and audition for distance communication, yet olfactory communications may occur in certain cases (McClintock, 1971).

7. Last, and most significant, scent marking should be more evident in gregarious species and have an obvious relation to sexual fitness and gene transmission. Pfeiffer (1962), for instance, found that the most extensive use of pheromones occurs in fish with complex social behaviors. Young (1950) pointed out a similar distinction between the social frogs, *Bufo,* and the semi-social groups, *Rana.* Likewise, the swamp rabbit (*Sylvilagus aquaticus*)

marks by chinning much more frequently than does the cottontail rabbit (*Sylvilagus floridanus* (Marsden & Holler, 1964). The former species is highly territorial and possesses a large chin gland, while the latter species is never observed to defend a territory and has a small chin gland. According to Mykytowycz (1970) similar differences exist in the lagomorphs (*Oryctolagus cuniculus* and *Lepus europaeus*). *Oryctolagus cuniculus* is highly territorial, has large anal marking glands, and marks frequently. *Lepus europaeus,* on the other hand, is a solitary-living hare with a wide home range. Its anal gland, as expected, is exceedingly small.

Ultimately, the importance of a scent gland must be judged by its contribution to the selective fitness of the individual or the population. In one way or another, a functional scent gland has a bearing on individual and species survival. Of course, not every glandular secretion will have the same function. Species differ in basic needs, and separate glands can serve different purposes. The social and ecological context will specify the function.

RESEARCH FINDINGS FOR INDIVIDUAL SPECIES

Columbian Ground Squirrel (Spermophilus columbianus)

Columbian ground squirrels are burrowing Sciurids often living in alpine or subalpine mountainous terrain. In North America they are found in regions inhabited by marmots, golden mantled ground squirrels, and pikas. The generic name suggests a granivorous diet, but in fact the diet is highly varied, including leaves, stems, flowers, tubers, seeds, nuts, and even insects (Steiner, 1970a).

Hibernation and aestivation permit the animals to live in harsh environments the year round. In the most severe climates hibernation may extend over a period of 7–8 months. The severity of the living conditions has led to a complex form of social organization and communication. Olfactory signaling, in particular, has become a prominent form of intraspecific communication.

The Columbian ground squirrel possesses several scent-producing or scent-bearing areas on the body (Steiner, 1973). It has a highly developed apocrine and sudoriferous glandular area in the mouth corners. The secretions of this gland, perhaps mixed with saliva, are applied to objects in the environment and transferred to conspecifics during a "greeting kiss." This same marking gland is found in the arctic ground squirrel, *Spermophilus undulatus,* and in ground squirrels of the genus *Citellus.* Mouth glands are also involved in the "tagging" of nuts stored by species of flying squirrels (Muul, 1970).

Ground squirrels also "cheek rub" with oily scent-bearing areas on the side of the head. A marking response typically begins with a mouth and cheek rub followed by a twisting of the body, which brings the ear and top of the head and shoulder areas into contact with the substrate. These latter areas are darker and oily in appearance, suggesting that they are secretory as well. Ultimately, even the more dorsal and posterior body areas are rubbed against objects. These too appear to be secretory or scent bearing. Thus, a full rub consists of a helical twist that sequentially brings all scent areas into contact with the objects of interest.

The Columbian ground squirrel also rubs the substrate with the throat and belly, occasionally flank marks, anal, and urine marks, and deposits eucrine secretions from the palmar areas of the feet while digging or scratching. The animal is virtually a marking machine. While none of the secretions has been biochemically identified, the variations seen in the location of glandular tissue and the diversity of behaviors promise exciting findings.

Typical of other species investigated, males mark more frequently and intensely than females, and marking is more intense at the peak of the reproductive season. Marking is directed at dirt mounds or den entrances and prominent landmarks, such as rocks, stumps, ridges, and earth or grass clumps. Scent marking is particularly evident on the periphery of the territory, which is visited frequently and consistently. André Steiner (1970a, 1970b, 1974), by years of concentrated field studies, has clarified a great deal of the social significance of these activities.

Group composition is variable, but a coterie generally has only one large dominant male, a small number of females, a variable number of yearlings, and the young of the year. The adult male is despotic, showing dominance over all animals of the group, and is a constant defender of the territory. He chases neighboring males that frequently intrude and constantly patrols and scent marks the territory. A great deal of the dominant male's time is spent visually surveying possible points of invasion. In many respects the social organization is similar to that found in prairie dog coteries (King, 1955).

Scent marking in the ground squirrel is almost the sole prerogative of the dominant male. During the early spring, the males emerge from hibernation several days before the females and engage in fights to establish territorial and mating rights. These activities appear to be correlated with increases in gonadal secretion and reach their highest intensity at the peak of the mating season. Males perform the anal drag, which leaves trails of urine or anal gland secretion, mainly after the testes become scrotal and the scrotum acquires a strong black pigmentation. At the same time, the males become very odorous and show a darkening of the face and other body parts. During hostile encounters the anal glands pulsate when the squirrel is frightened. It has not been definitely established that testosterone is the provoking hormone, but that is probably the case. Interestingly, marking by adult females increases during pregnancy and lactation (Kivett, 1975), a finding in accord with observations of the gerbil *Meriones unguiculatus*.

Ground squirrel marking functions are not understood in their entirety, but they show strong relations to recognition behaviors and agonistic encounters. The mouth kiss occurs among all members of a group and seems to be associated with greeting responses and individual recognition. Young animals and sometimes adults solicit food from the mouth pouch by probing the corners of the mouth. This may have become ritualized into a signaling kiss. In most cases it is the dominant animal that takes the initiative and makes the final approach for the kiss. The greeting behavior occurs whenever animals have been separated or after provoking raids by other territorial males. It may be a way of maintaining social cohesiveness and disseminating group odors. This function may be complemented by substrate marking with the mouth and other body glands, by belly dragging during comfort activities, and by self- and allo-grooming, which also involve scent marking and scent sharing.

In Columbian ground squirrels, the dominant male in each community performs nearly all the territorial and group marking. The introduction of strange animals evokes high levels of marking, and in a general way, locomotor activity is positively associated with the frequency of marking. Cheek and mouth rubbing have been observed to follow a fight. Trails of anal gland secretions and urine are investigated avidly, and areas marked by intruders are quickly covered by resident marks.

Territorial marks do not prevent neighboring males from invading the coterie, a universal finding among scent-marking mammals. They do, however, seemingly lower the invader's flight threshold and clearly indicate a willingness of the dominant male to defend its territory. Some evidence shows that dominant males mark more frequently and are more aggressive in the presence of a reproductively active female and a rival male than in just the presence of the rival (Kivett, 1975). Obviously there is a close relationship between territorial marking, reproductive functions, and agonistic activities.

The Columbian ground squirrel investigations are continuing with the work of Steiner and his collaborators and promise to be highly informative. The most crucial problem in scent-marking studies is relating marking to various social activities and reproductive success. To a degree not possible with many other species, this information is becoming available with the ground squirrel. This fascinating species offers the investigator the necessary degree of social complexity and stability associated with a variety of scent glands and marking activities. It is diurnal, accessible in its natural environment, yet lives comfortably in the laboratory. The reproductive cycle is short enough to allow observations over several generations, and the animal is large enough to allow detailed physiological studies. The Columbian ground squirrel may indeed lead us to our best understanding of social behavior and olfactory communication.

Mongolian Gerbil (Meriones unguiculatus)

The Mongolian gerbil is a native of northeast China and Mongolia. It lives in a wide assortment of ecologies but is primarily associated with arid and semi-arid environments. Its family unit is unknown, but it appears to live in small groups dominated by a single male.

Both the male and female possess a ventral scent-marking pad which they use to mark their environment. Gland size and marking frequency are normally sexually dimorphic in favor of the male (Thiessen, 1973). Marking is dependent upon olfactory as well as visual cues (Baran, 1973; Baran & Glickman, 1970; Thiessen, Lindzey, & Nyby, 1970). Castration in both sexes results in a striking reduction of ventral scent marking and a total elimination of the ventral sebaceous pad. Figure 1 shows the effects of castration and hormone replacement on marking frequency. Testosterone is probably the active hormone in males and estrogen (or estrogen plus progesterone) in females, although a wide array of steroids are effective in castrates of both sexes (Thiessen, Friend, & Lindzey, 1968; Wallace, Owen, & Thiessen, 1973; Yahr & Thiessen, 1972).

Testosterone implanted into the preoptic brain region of male castrates (Thiessen & Yahr, 1970) and estrogen implanted into the same area of female castrates (Owen, Wallace, & Thiessen, 1974) reinstate the behavior. The steroids may be acting on the genome of the preoptic cells, as agents which prevent DNA activity or protein synthesis in

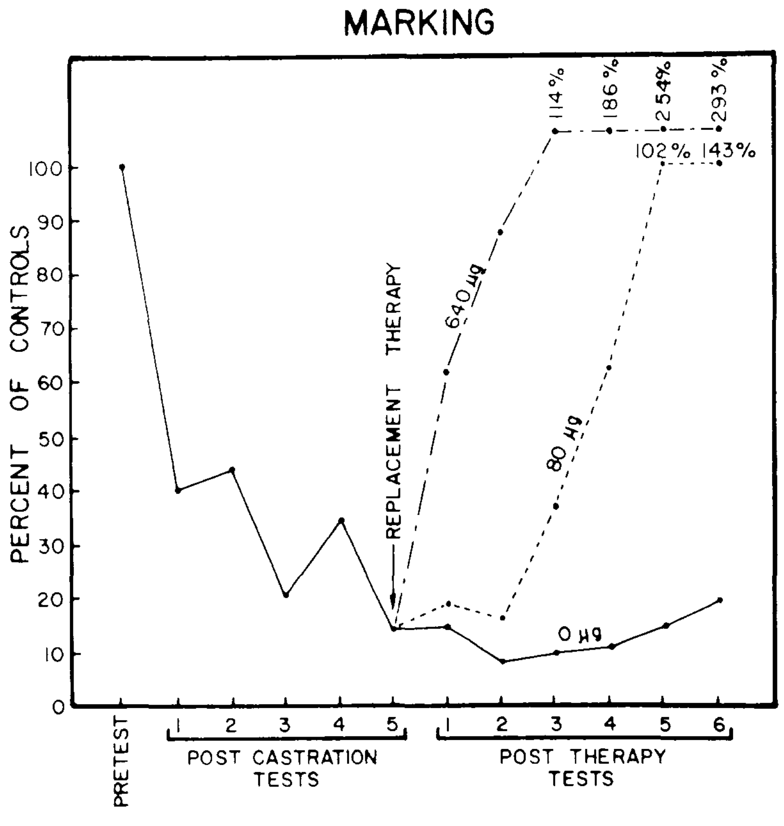

FIGURE 1. Change in ventral scent gland marking following castration and replacement with 80 or 640 µg testosterone propionate in the Mongolian gerbil. (Testing periods conducted every 3 days; hormone injections given subcutaneously every 3 days.)

the male prevent testosterone from acting (Thiessen, Yahr, & Owen, 1973).

One of the initial responses to the scent gland secretions is exploration; however, this response habituates quickly and is not reinstated unless the sebum becomes conditioned to social activities in the population. High male markers generally become dominant in paired encounters, but regardless of the initial marking, the male becoming dominant marks at high levels and the subordinate male stops marking altogether (Thiessen, Owen, & Lindzey, 1971). Subordinate animals still possess the ability to mark and will do so in an area in which they have not experienced defeat. Hence, it appears that scent marking is closely associated with agonistic activities and the scent signal can be used differentially depending on the social context. From several observations it seems that the scent gland secretion can be used to denote social status, as trail markers leading to food, as cues to identify sex, as territorial barriers, and as stimuli for individual recognition (Halpin, 1974; Thiessen, 1973).

During gestation and especially lactation the female marks at very high levels. This change is correlated with nest building, maternal care, and increased aggression (Wallace et al., 1973). The mother can identify her pups by the scent she marks on them, and at the same time, the pups can identify their mother on the basis of olfactory cues. It appears, therefore, that female scent marking may be important for maternal care and nest defense. The same hormones, estrogen and possibly progesterone, coordinate all of these related behaviors.

Recent studies using conditioning techniques, exploratory tests, thin layer and gas chromatography, and mass spectrophotometry indicate that the primary scent gland pheromone in the male (and probably the female) is phenylacetic acid (Thiessen, Regnier, Rice, Goodwin, Isaacks, & Lawson, 1974). Other volatiles are present among the many components found, and may account for the ability of individuals to recognize each other on the basis of sebum cues (Halpin, 1974).

In brief, the social functions integrated by phenylacetic acid are controlled by gonadal hormones acting on selected cells of the preoptic area. Further research is needed to specify the range of social behaviors affected and the interaction between olfactory stimuli, brain processes (particularly neurotransmitters), and behavior.

The Mongolian gerbil also secretes a pheromone from the anterior nares (Thiessen, Clancy, & Goodwin, in press). It originates from the Harderian gland, situated directly behind the eye ball, and is transported down the Harder–lacrimal canal to exit at the tip of the nose. The pheromone is associated with the fluorescent pigment protoporphyrin and is easily visualized under long wave irradiation.

Males and females exposed to novelty or to each other face groom the pheromone onto heat-sensitive areas of the face such as the nose, mouth, chin, and paw, using saliva as a base for the fluorescent painting. The half-life of the fluorescence is approximately 1–2 minutes, corresponding to its pheromonal effects. The signal is short lived. Saliva is used not only as a base for spreading the Harderian material but also as a means of decomposing the signal within 2 minutes. Denatured saliva does not possess this quality, suggesting that an enzyme normally decomposes the pheromone.

The Harderian material stimulates investigation and triggers grooming in conspecifics. Its function is debatable but appears to relate to individual recognition and dominance. Dominant males in pairs groom more frequently and secrete greater amounts of the pheromone. Moreover, Harderianectomized males always become submissive in paired encounters.

Our notion as to the function of the Harderian pheromone is summarized in Figure 2. At this point we believe that the key to understanding the mechanisms and function of the pheromone activity lies in the thermoregulatory processes associated with grooming. Whenever body temperature rises, as in social interactions and general arousal, secretion of Harder's pheromone and grooming are evoked. Heat-sensitive areas of the body then broadcast the volatile signal until it is broken down by enzymes in the saliva. At the same time, saliva acts in evaporative cooling of the organism. Submissive animals transmit fewer signals, groom less, and may have a more difficult time dissipating body heat—surely a social disadvantage. The pheromone has not been identified. It could be a lipid, several of which seem to be present in the material, or it could be the pigment protoporphyrin itself. The total extract has a floral odor.

Similar relations between grooming and the spread of secretion have been seen in Sprague-Dawley (Holtzman) albino rats, the female golden hamster (*Mesocricetus auratus*), and other species of gerbils—*Meriones tristrami, M. libycus,* and *M. shawi.* Deer, antelope, and other species often have orbital and preorbital secretions used for object marking. These may be Harderian in origin. The widespread appearance of Harderian glands in many species and the near-ubiquitous behaviors of facial grooming, body investigations, and nuzzling suggest that Harder's pheromone may be a general communication signal in a wide range of vertebrate species.

Golden Hamster (Mesocricetus auratus)

Virtually nothing is known about the social organization of wild hamsters (*Mesocricetus auratus*), although in captivity adult hamsters are extremely intolerant of each other (Johnston, in press-c). In the wild, some hamsters live a solitary existence, with each individual maintaining a separate burrow (Eibl-Eibesfeldt, 1953d). Both males and females have clearly defined oval regions of enlarged, pigmented sebaceous glands on the dorsal portion of each flank, and secretions from the glands are deposited on objects in the environment by a highly stereotyped behavior pattern. The marking animal arches its back and rubs one side against a vertical surface. The ears are erect and the tail is in a horizontal or slightly raised position during the marking behavior. Biochemical analyses of the components of the gland secretions have not been performed. In addition to scent marking with the flank gland, female hamsters exhibit vaginal marking with a clear substance from pouches adjacent to the vagina. A thin layer of material is deposited as the anogenital region is pressed against the substrate while the female moves forward. As with flank marking, the animal's tail is tilted upward and the ears are erect.

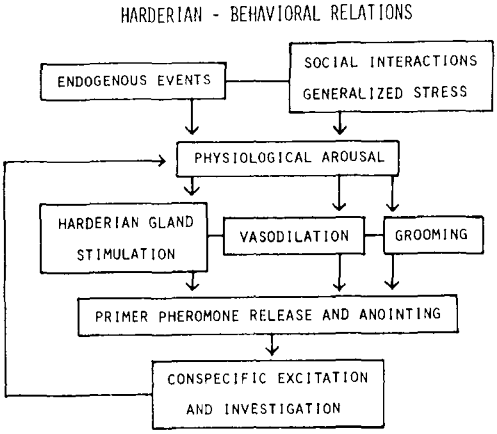

FIGURE 2. Proposed mechanisms for Harderian pheromone secretion and behavioral responses.

The bulk of the evidence indicates that flank marking in both sexes is positively correlated with agonistic behavior and negatively correlated with the tendency to flee. After two animals of either sex meet and establish dominance, flank marking is low in the subordinate and high in the dominant animal. In fact, in many cases marking scores can be used to predict the dominance relationship between two animals. However, marking should probably not be construed as a threat display because it normally occurs after contact has occurred and is typically directed away from the other animal (Johnston, in press-c). In most instances subordinate males never mark until separated from the dominant male, and if they mark at all, it is at very low levels. It is still possible that the odor left by the scent mark serves as a threat or warning signal.

Flank marking by males after encounters with females depends on the stage of the females' estrous cycle. Female hamsters show a 4-day pattern of cyclicity. The male's marking is very low on the days of estrus and metestrus and high on the other 2 days. Apparently only olfactory cues from the females are necessary for the modulation of male marking; however, the differences between the days of the estrous cycle are intensified if there is physical contact between the male and female (Johnston, in press-a). Variations in female flank marking do not appear to be related to reproductive status, although estrous females rarely mark during or after encounters with either males or females (Johnston, Note 4).

Vaginal marking peaks the day of proestrus, is very low the day of estrus, intermediate the subsequent 2 days, and low from pregnancy through the final stages of lactation (Johnston, 1972, 1974). Normally females vaginal mark more frequently in encounters with males than with females. The strong relationship between vaginal marking and a state of "reproductive readiness" suggests that the secretions may serve as a sexual attractant to the male. Indeed, in a two-bottle choice situation, males show a preference for vaginal secretions versus a clean bottle in 91% of all trials. "Inappropriate partners" (anesthetized or gonadectomized animals) can be made attractive when the secretion is applied to their genital regions, and experienced as well as inexperienced males will attempt to mate with the stimulus animals (Murphy, 1973). There is some evidence that vaginal secretions may have appeasement functions: During encounters between females, the subordinate female vaginal marks more than the dominant female.

In this species, flank marking may be triggered by the odor of another animal or its scent marks. For instance, males will flank mark more in an empty home cage of another male or female (unless the female is in estrus), and the male's marking is apparently directed toward one or two spots, which may be the resident's marking area. Although removal of the gland does not affect marking behavior, males mark less in the cages of glandectomized males (Johnston, in press-b). Females vaginal mark most in the presence of a male's odor, least in a female's cage, and at intermediate levels in clean cages; however, they flank mark most in a female's cage, least in a male's, and at intermediate levels in clean cages.

The size and pigmentation of the flank gland appear to be controlled by androgen in both male and female hamsters. Castration of males results in reduced gland size as well as reduced pigmentation, and both measures respond to testosterone propionate but not to estradiol benzoate. Ovariectomy has no effect on the state of the female's flank gland, and there is no response to estradiol benzoate. However, when testosterone propionate is administered to females, the amount of pigmentation is increased to levels comparable to those found in males. Gland size is also increased, although it remains smaller than in males (Vandenbergh, 1973). As might be expected, ovariectomy does abolish vaginal marking as well as the attractiveness of the vaginal secretion to males.

The hormonal control of the flank-marking behavior is partly understood. Flank gland size (Drickamer, Vandenbergh, & Colby, 1973a, 1973b) in both males and females is positively correlated with percentage of fights won (see Table 3); however, other data indicate that dominance and scent marking are not absolutely dependent on the presence of testosterone (Tiefer, 1970; Whitsett, 1975).

There are many interesting possibilities for further research. The hamster shows the clearest response to sebum of any of the rodent species studied and so would be an excellent model for the biochemical analysis of the sebum. Recently dimethyl disulfide has been identified as a major active component of the vaginal secretions (Singer, Agosta, O'Connell, Pfaffmann, Bowen, & Field, 1976). There is some ambiguity regarding the hormonal control of scent-marking and related behaviors in the hamster (Whitsett, 1975), and more research is needed to clarify the parameters in the area. Most important, the available laboratory information must be related to the ecology of the hamster in its natural environment.

Guinea Pig (Cavia porcellus)

The guinea pig is indigenous to South America. Six species are represented. *Cavia porcellus* is one of the most popular research species and is providing interesting data on scent-marking behavior. This rather rotund species was already domesticated by the Incas, who bred it as a food delicacy and as a sacrificial animal. In the wild, cavies are found in a variety of habitats but seem to prefer dense vegetation, in which they use regular beaten tracks. They communicate by a variety of means including high-pitched squeaking and pheromones. The young are born in an advanced state of development, which may prove to have a bearing on the development of communication systems. Male guinea pigs have two prominent sebaceous skin glands in the supracaudal and perineal areas. Both appear to be androgen dependent, as they regress following castration (Beauchamp, 1974; Martan, 1962; Martan & Price, 1967).

Beauchamp (1974) has recently made some significant observations on the scent-marking behavior of the male. The studies to date have concentrated on the perineal gland. A secretory material from this gland is deposited on the substrate during a perineal drag. Both males and females demonstrate this behavior, although it is more common in the male (Kunkel & Kunkel, 1964). Briefly, what Beauchamp found is a relationship between sebum production, agonistic behavior, and dominance status in males living in mixed-sex groups. During social interactions the anal–genital pouch containing the sebaceous sebum is extruded, allowing the sebum to be placed on the substrate. The pouch can be manually opened and the sebum removed and weighed on cotton swabs.

Animals living in mixed-sex groups show an increase in sebum production from that of animals living in isolation, with the dominant male showing the greatest increase. Production can increase as much as 50 mg. Interestingly, while there is a strong correlation between male dominance and sebum production in groups ($r = .75$), sebum production before grouping cannot be used as a predictor of dominance ($r = .33$). This is contrary to data obtained with the rabbit, hamster, and Mongolian gerbil.

As expected, the frequency of the perineal drag is significantly correlated with dominance status ($r = .79$). A less common observation is that there is a substantial correlation between sebum production and frequency of scent marking ($r = .70$). Thus, the behavior, metabolic events leading to sebum formation, and social dominance are closely linked and probably under the influence of testicular androgens. These events appear developmentally around 4–5 weeks of age, also suggesting a relationship to gonadal maturity.

The association between scent marking, sebum production, and agonistic behaviors is seen most clearly when shifts of dominance occur. In one test situation, in which intersex groups were observed for 6 months, 17 changes in dominance were seen. In 82% of these cases, an upward shift in special position was related to increased sebum production and a downward shift in status was related to decreased sebum production. While other functions of scent marking have been noted, such as individual identification (Beruter, Beauchamp, & Muetterties, in press), one of the major functions is related to aggression. Chemical identification of the sebum has not been accomplished, and there are still many points that need investigation. At this point, however, it is obvious that *Cavia porcellus* presents a picture not unlike many other scent-marking mammals.

TABLE 3

CORRELATES OF SOCIAL RANK IN MALE AND FEMALE GOLDEN HAMSTERS

Subject	Social rank	Mean percentage wins	Mean gland index (e.g., size)	Mean gland marks
Male	1	98.0	668	53
	2	34.1	639	18
	3	19.0	613	10
	4	5.4	595	9
Female	1	93.5	366	96
	2	44.9	310	67
	3	19.5	270	26
	4	6.2	246	7

Note. Data taken from Drickamer, Vandenbergh, and Colby (1973).

Pika (Ochotona princeps)

The diurnal species of Pika found in North America are mostly restricted to mountain rock slides (Broadbooks, 1965). Animals of the best-studied species, *Ochotona princeps,* are quite territorial, and advertise and defend their territories with distinctive vocalizations (Broadbooks, 1965). Females have either one or two litters during a summer and juveniles are forced to disperse around August (Markham & Whicker, 1973; Millar, 1970). Very little is known about scent marking and its relative importance to these animals, although the pika does have an apocrine cheek gland and associated behavior. Males and females come together in the late spring and summer to breed; however, adults generally keep separate territories which are rigidly defended, by vocalizations (Broadbooks, 1965). Barash (1973) found that the territories were marked with the cheek glands and that 72% of all marks were along the perimeter of the territory. The cheek glands are larger in males than in females, and are larger in estrous females and reproductively active males (Sharp, Note 5). Forty-nine percent of all marks observed by Barash (1973) were in June, which coincides with the time of mating. Sharp (Note 5), however, found that females showed a higher incidence of cheek rubbing in July. She also noted that juvenile males cheek marked more than any other group, with a peak in August. Juveniles mark most often inside intensively used areas, while adults mark more outside the areas of intensive use.

Although data are scanty regarding the significance of scent marking and the importance of olfactory communication in the pika, those data which are available are quite interesting. If the finding that scent marks are concentrated at the territorial borders holds true, this would be strong evidence for the use of scent marks in maintaining territories. The importance of vocalizations in the pika, especially their use in the maintenance of territories, has been emphasized by many authors. Studies designed to elucidate the relationship between auditory and olfactory communication could provide valuable information.

European Rabbit (Oryctolagus cuniculus)

The life style of the European rabbit (*Oryctolagus cuniculus*), involving a strong social and territorial organization, has been extensively studied by Mykytowycz and his co-workers (Mykytowycz, 1973, 1974; Mykytowycz & Goodrich, 1974). Groups of rabbits, typically consisting of several males and females, confine the majority of their activity to a group territory with a warren, a central burrow with several entrances. Each member of the group spends most of its time in a particular area within this territory. There is overlap between these individual spaces, and the more dominant males control the largest amount of space. In fact, the area controlled by the dominant male often coincides with the group territory. Dominant females do most of the breeding and as a result of being confined with litters, they tend to have the smallest areas. Females compete for possession of extensions to the warren, known as breeding chambers, in which they give birth to and nurse their kittens. The offspring of the dominant females, with access to a breeding chamber, have a higher survival and growth rate than the young raised by lower ranking females. Subordinate females are often forced to drop litters in isolated spots at some distance from the warren (Mykytowycz, 1968).

Lipid extracts from the anal gland and the apocrine portions of inguinal glands have the characteristic "rabbity" odor. Analyses of gland extracts have shown that there are differences in the chemical composition between different glands, as well as sex differences within the same type of gland. Negatively charged proteins are present in chin and anal gland secretions from both sexes, but higher concentrations are present in secretions from males. Although carbohydrates bound to protein are present in all secretions, they constitute a major portion only of males' anal glands. The chin gland, whose secretions have no odor to man, contains proteins and carbohydrates. Secretions from the sebaceous portion of the inguinal gland have a very similar chemical composition across all individuals, suggesting that the sebum may function as a fixative (Goodrich & Mykytowycz, 1972).

Chin gland size and secretory activity fluctuate throughout the year, and both are maximum during the breeding season. The anal gland is also largest and its secretions have the strongest odor during this time (Hesterman & Mykytowycz, 1968). There is some evidence that marking behavior may be used during mating; however, the strongest evidence links the chin and anal glands to social status. Chinning may be used as a predictor of the dominance relationship between two animals, and the frequency of chinning increases after aggressive behavior. Animals with the highest social rank chin mark more often and have larger chin, as well as anal, glands. Dunghills are frequented more often by males than by females, and males of high social rank pay more visits than do subordinates (Mykytowycz & Gambale, 1969).

Mykytowycz has proposed that anal glands are used to provide homesite odors by way of the scented fecal pellets found in dunghills, and that these homesite odors have a "confidence-giving" effect. This confidence effect is demonstrated when two rabbits meet in a territory contaminated with the odor from one of them. The rabbit whose own odor is present wins fights more often (69% of the time for males and 66% for females) and initiates more interactions. There are also more wins in the presence of an odor from the animal's partner (Mykytowycz, 1972, 1974). Evidence for homesite recognition on the basis of odors from the dunghills is found when animals react to the presence of a strange dunghill by cessation of eating, sniffing, and marking with their own fecal pellets (Mykytowycz & Hesterman, 1970).

Gland odors are also important for individual recognition. Males chin and lick kittens; and adults of both sexes identify their own from strange kittens on the basis of odors. The young are also able to recognize their mother's odor; and the presence of a group odor on the kittens protects them from aggression. Females tolerate their own kittens, harass others of the same colony, and kill kittens from other colonies, in a laboratory situation (Mykytowycz & Dudzinski, 1972). The inguinal gland secretions can also be used for individual recognition, as females will attack their own kittens that have been smeared with inguinal secretions from another animal. They will not, however, attack kittens that have been smeared with another animal's anal gland secretion (Mykytowycz & Dudzinski, 1972).

The presence of a strange scent in the home territory is frequently a trigger to marking behavior in rabbits. Males chin mark strange kittens, and all animals chin more in their own territory and most intensely when confronted with foreign feces on their own ground. Animals presented with a foreign dunghill will excrete fecal pellets of their own in order to mark it (Mykytowycz & Hesterman, 1970).

The chin, anal, and inguinal glands of the European rabbit are apparently under the control of steroid hormones. They are larger in males than in females, and the chin gland of a socially dominant male is twice that seen in subordinate males. Males also mark more than females and dominant males mark more than subordinate males, both in the lab and in the wild. The first evidence of chin marking and the enlargement of the gland occurs at puberty, the same time that sex differences in gland size become apparent. The data indicate that testosterone (or other androgens) facilitates both the secretory activity of the glands and the marking behavior, while estradiol exerts an inhibitory effect. When animals are gonadectomized at 7 weeks, chin and anal gland weights are reduced in males and increased in females. Animals of both sexes respond positively to male hormones, and estradiol causes decreased gland weight in intact males (Wales & Ebling, 1971; Mykytowycz, 1966a; see Table 4).

Possibilities for future research regarding the importance of odors in the life of a rabbit are numerous. Other aspects, concerning the confidence-giving effect of homesite odors, may be tested. For example, are familiar odors necessary for the female to become receptive, mate, and successfully rear young, and are they necessary for proper growth and development of the young? It has been suggested that inguinal gland secretions may be more important in individual recognition, while chin and anal glands contribute more to a group odor. Further research on these questions may indicate whether this is a true dichotomy of function, or may clarify the areas of overlap between individual and group odors. There is no information regarding brain control of marking behavior. Finally, further analyses of the olfactory components of the glandular secretions and testing of these com-

TABLE 4

RELATIONSHIP AMONG CHIN GLAND WEIGHT AND HORMONAL STATUS IN MALE AND FEMALE RABBITS

Subject	*N*	Chin gland weight (mg)	Frequency of chinning in 10-min trial	No. seconds spent chinning in 10-min trial
Intact males	7	1,000	14.3	46.3
Castrated males	5	379	1.0	3.6
Intact females	4	242	4.0	7.0
Castrated females	7	376	.0	.0

Note. Data taken from Mykytowycz (1966).

ponents in behavioral situations will provide valuable information on the nature of olfactory communication.

Sugar Glider (Petaurus breviceps papuanus)

The importance of olfactory information in the recognition of group members can be clearly seen in the sugar glider (*Petaurus breviceps papuanus*). These interesting arboreal marsupials are nocturnal and live in communities consisting of several males, females, and their offspring. Each community has at least one dominant male that is responsible for most of the mating, territorial patrolling, scent marking, and aggression. Individual and community-specific information is transmitted through odors, and intraspecific aggressive behavior is seen only between different communities (Schultze-Westrum, 1969).

Adult male sugar gliders possess three distinct odor-producing areas: a frontal gland, a sternal gland, and the anogenital region, which can produce odors via urine or secretions from the proctodael and paraproctal glands. It is possible that odors from the saliva also have information content. Although females do not have frontal or sternal glands, they possess scent glands in their pouches which are active from shortly before parturition until the young leave the pouch.

The community odor is transmitted in a somewhat unusual and fascinating manner. One animal clasps the neck of a second animal and at the same time, the first animal twists its head so that it is facing upward. The first animal then rubs its forehead on the chest of the second. If the first animal is a male, this behavior transfers the secretions from his frontal gland to the chest area of the second animal. If it is a female and the second is a male, the secretions from the male's sternal gland are transferred to the female's forehead (Schultze-Westrum, 1969). The importance of these shared odors is clearly demonstrated when an animal is removed from the community for several days. Upon its return to the group, this animal will be promptly marked, unless it has been marked by a strange male, in which case the animal will be attacked (Ewer, 1968).

Odor differences in the secretions from one gland imply the possible use of olfactory information for individual recognition (Schultze-Westrum, 1969). The pouch odor of a mother is attractive to a newborn sugar glider. The young are not able to distinguish their own from other mothers until about Day 74, which is the time they normally begin to leave the pouch. At this time they are able to recognize their own mother, and by Day 94 they are able to discriminate between the odors of two communities.

Marking can be triggered by removing the dominant male from a community (Schultze-Westrum, 1969). This leads to increased marking, patrol activity, mating, and aggression by other males. Although there is no specific information on the control of scent marking in the sugar gliders, the sexual dimorphism of the glands, as well as the correlation marking behavior and social status, suggests that they are under the control of androgens. However, more research is needed to verify this hypothesis. The behaviors directed toward a colony member who has been marked with a "strange" odor appear to be quite predictable and could be used as a bioassay for the analyses of the gland secretions.

Even-Toed Ungulates (*Order Artiodactyla*)

Many even-toed ungulates have a variety of scent glands, including pedal, metatarsal, tarsal, inguinal, rump, and facial glands. While some research has been done with tarsal and other body glands, clearly the major focus of investigation has centered on the facial glands. The subauricular patch below the ear in the pronghorn Antilocaprid and the preorbital gland in many Cervidae and Bovidae species are now beginning to receive attention.

Research opportunities are superb, as the ungulates are almost worldwide in distribution and show a great variety of social organizations (Geist, 1974). There are one hundred ninety-four species of even-toed ungulates alive today. Here are man's most important domesticated animals, including pigs, hogs, sheep, cattle, camels, yaks, llamas, and reindeer. Unfortunately many of the wild counterparts are endangered, such as the deer,

TABLE 5

ARTIODACTYLA SHOWING PREORBITAL SCENT GLANDS

Genus and species	Common name
Family Cervidae (deer)	
Axis Axis	Axis deer or chital
Blastocerus campestris	Pampa deer
Blastocerus dichotomus	Marsh deer
Cervus axis (*Axis axis*)	Chital or spotted deer
Cervus duvauceli	Swamp deer
Cervus elaphus	Red deer
Cervus hortulorum	Pekin deer
Cervus kansuensis	Kansu deer
Cervus maral	Caucasian red deer
Cervus unicolor	Sambar
Elaphodus cephalophus	Chinese tufted munjak
Hippocamelus bisulais	Chilean huemul
Hydropotes inermis	Chinese water deer
Mayama bricenii	Brocket deer
Mayama nemorioagus	Wood brocket
Mayama nemorivagus	Wood brocket
Muntiacus muntjak	Black-footed munjak
Odocoileus virginianus	White-tailed deer
Pudu pudu	Pudu
Rangifer arcticus	Kensai caribou
Rangifer tarandus	Reindeer
Family Bovidae (antelope)	
Adenota kob	Buffon's kob
Alcelaphus Lichtensteini	Lichtenstein's hartebeest
Antidorcas marsupialis	Springbok
Antilope cervicapra	Indian blackbuck
Boselaphus tragocamelus	Nilgai
Capricornia sumatraensis	Serow
Cephalophus caerulus	Blue duiker
Cephalophus dorsalis	Bay duiker
Cephalophus maxwelli	Maxwell's duiker
Cephalophus melororheus	Gray's duiker
Cephalophus nigrifrons	Black-footed duiker
Cephalophus silvicultor	Yellow-backed duiker
Family Bovidae (antelope)	
Cephalophus spadix	Abbott's duiker
Damaliscus albifrons	Blesbok
Damaliscus hunters	Hunter's antelope
Damaliscus lunatus	Sassaby
Giazella bennetti	Persian gazelle
Giazella cuvieri	Morocco gazelle
Giazella dorcas	Isabellini gazelle
Giazella granti	Grant's gazelle
Giazella marica	Arabian gazelle
Giazella muscatensis	South Arabian gazelle
Giazella pelzelni	Pelzelna's gazelle
Giazella rufifrons	Korin gazelle
Giazella soemmerriagii	Soemmerring's gazelle
Giazella subgalturosa	Yarkland gazelle
Giazella thomsonii	Thompson's gazelle
Hippotragus niger	Sable antelope
Lithocranius walleri	Gerenuk
Madoqua phillipsii	Lord Phillip's dik-dik
Nesobragus moschatus	Akeley's suni antelope
Oreotragus areotragus	Kilipspringer
Ourebia nigricaudata	Black-tailed oribi
Ovis dalli	Dall's sheep
Ovis musimon	Muflon
Ovis poli	Thian shan sheep
Pantholops hodgsoni	Tibetan antelope
Raphicerus campestris	Steinbok
Rhynchotragus kirkii	Nyika dik-dik
Sylvicapra grimmia	Bush duiker
Saiga tatarica	Saiga antelope
Sylvicapra coronata	Grey duiker
Tetracerus quadricornis	Four-horned antelope
Family Suidae (pig)	
Hylochoerus meinertz	Black forest hog

antelope, giraffe, and okapi. Hopefully we will learn much more about their social adaptations before they disappear from our species catalog.

Pocock (1910) did a great service by describing the variety of glands in dozens of Cervidae and Bovidae species. Since active scent gland marking is the topic of interest here, we have tabulated data in Table 5 on the preorbital gland cited by Pocock, other investigators (Schaller, 1967; Whitehead, 1972), and our own observations. It is not established how many of these species actually use these glands for scent marking, but it must be many if not all. For those species that have been observed, the typical behavior involves shaking the head, thrashing the bushes, and touching the preorbital pocket to twigs or blades of grass (Schaller, 1967). Sometimes the smeared secretion is transferred back to the head and body by rubbing, and occasionally animals mark each other while nuzzling and sniffing.

The ultrastructure of the gland has not been described and in only one case has the secretory material been identified (see below).

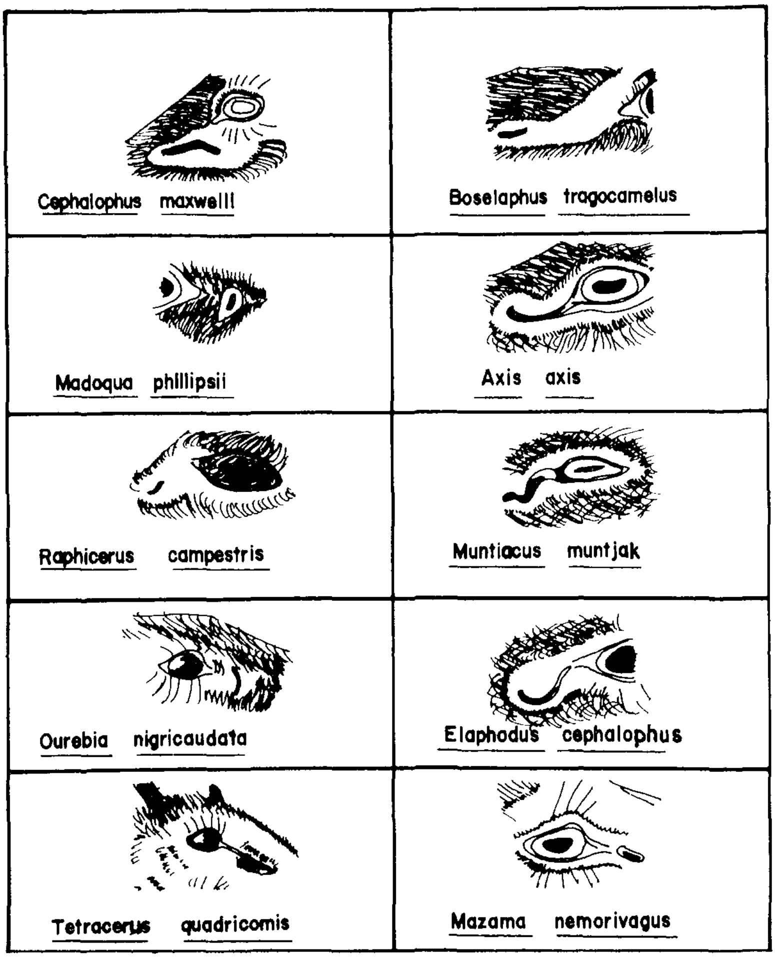

FIGURE 3. Anatomical juxtaposition between preorbital gland and anterior corner of the eye in representative species of Cervidae and Bovidae. (See Table 5 for common names.)

Anatomically the gland is in proximal association with the anterior aspect of the eye (see Figure 3). In several species of gazelle, the black-tailed oribi, the springbok, the four-horned antelope, red deer, wood brocket, and blackbuck the gland is valvular and opens when the animal becomes excited. In other Bovidae and Cervidae the preorbital glands are large but immovable. In either case, the origin of the secretion may not be exclusively from the gland itself but may be from the Harderian–lacrimal glands situated behind the eyeball. This has not been established but could explain the intimate association between the facial glands and the eye.

Again the evidence is not complete, but the preorbital glands are generally larger and more secretory in adult males, especially during the rutting season. The subauricular gland in the pronghorn is evident only in the male and is clearly associated with aggressive and sexual activities (see below). The facial glands appear to be under the exclusive control of gonadal activity.

The only comparative study of preorbital scent marking and social behavior of ungulates is reported by Schaller (1967). The chital (*Axis axis*), barasingha (*Cervus duvauceli*), sambar (*Cervus unicolor*), blackbuck (*Antilope cervicapra*), and hog deer (*Axis porcinus*) all scent mark during aggressive and sexual encounters. Interestingly, there is

TABLE 6

COMPARISON OF SOME MALE AGGRESSIVE AND SEXUAL BEHAVIOR PATTERNS IN SEVERAL INDIAN UNGULATES

Behavior pattern	Chital	Barasingha	Sambar	Hog deer	Blackbuck
Preorbital gland marking	Yes	Yes	Yes	Yes	Yes
Thrashing bushes with horns	Yes	Yes	Yes	Yes	Yes
Rubbing bark off tree trunks with horns	Yes	Yes	Yes	?	No
Preaching	Yes	No	Yes	No	No
Pawing with foreleg	Yes	Yes	Yes	Yes	Yes
Defecating on dung piles	No	No	No	No	Yes
Wallowing	No	Yes	Yes	No	No
Stamping ground	No	No	Yes	No	No
Head-up display	Yes	Yes	Yes	Yes	Yes
Head-down display	Yes	No	?	Yes	No
Lateral display	Yes	Yes	Yes	Yes	Yes
Horizontal neck display	No	No	No	No	No
Low-stretch display	Yes	Yes	Yes	?	No
Sparring	Yes	Yes	Yes	Yes	Yes
Loud rutting call	Yes	Yes	Yes	No	No
Flehmen	Yes	Yes	Yes	Yes	Yes

Note. Data taken from Schaller (1967). ? = data indeterminate.

no distinction between scent marking in territorial species (sambar and blackbuck) and nonterritorial species (chital, barasingha, and hog deer), but there are a number of other behaviors that are inevitably associated with marking (Table 6).

For all of these species, preorbital marking is more frequent in the male and is closely related to the rutting season. Schaller suspected that the rut, scent marking, aggression, courting behaviors, and antler growth are intimately linked to testicular cycles. Since, however, the breeding seasons differ widely for these various species inhabiting the same general ecology, the proximal stimuli cannot be the same. In some cases a seasonal reduction in light may precipitate the rut, whereas in other cases an increase in light may be important. Temperature and vegetative fluctuations can also be significant. Obviously, more detailed investigations are needed.

Pronghorn (Antilocapra americana)

The pronghorn antelope is the last surviving representative of the Antilocapridae family, which flourished in the Pleistocene. It shares many features with the African bovids, occupying similar niches, even though it resides exclusively in North America.

There are two prominent scent glands in the pronghorn (Moy, 1970): a rump gland, which is neither sexually dimorphic nor seasonal; and a subauricular gland, which is found only in the males and is influenced by the seasons. The subauricular glands are located beneath the ears in an area of thickened skin. Sebaceous and apocrine tissue is highly developed in the central portion and secretes milky-tan globules. The peak of glandular activity corresponds with peaks in testicular activity, horn growth, and the breeding season in mid-September to October (Moy, 1970; O'Gara, Moy, & Bear, 1971). These striking relations are shown in Figure 4.

The secretory composition of the subauricular secretion has recently been identified (Müller-Schwarze, Müller-Schwarze, Singer, & Silverstein, 1974). Eight compounds have been isolated: (a) 2-methylbutyric acid, (b) isovaleric acid, (c) 13-methyl-1-tetradecanol, (d) 12-methyl-1-tetradecanol, (e) 13-methyltetradecyl-3-methylbutyrate, (f) 12-methyltetradecyl 3-methylbutyrate, (g) 13-methyltetradecyl 2-methylbutyrate, and (h) 12-methyltetradecyl 2-methyl-butyrate. It is possible that the esters (e, f, g, and h), which are found in abundance, are the precursors for the acids (a and b) and that the alcohols (c and d) act as diluents and release regulators for the more volatile acids. When males are exposed to objects smeared with a succession of these eight components in varying

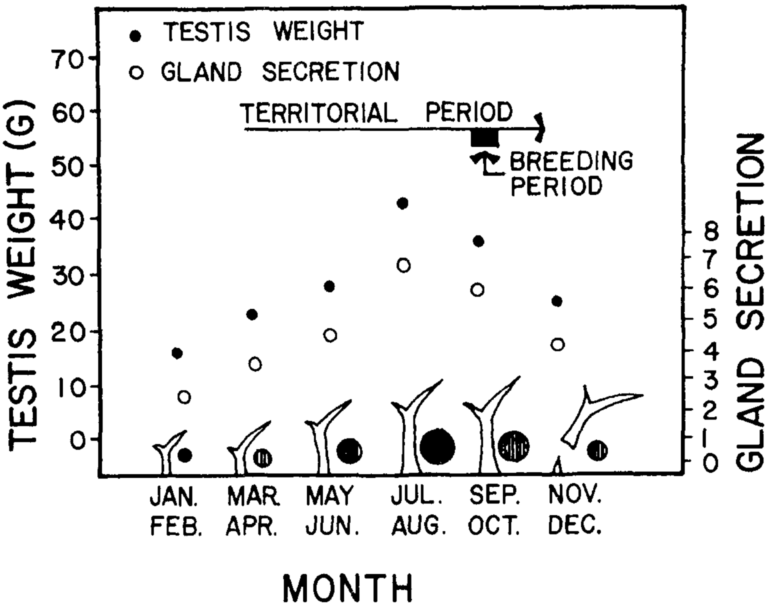

FIGURE 4. Seasonal changes in paired testis weight and size, subauricular gland secretion, spermatogenesis, and horn growth. (The ovals represent testis size and are shaded to indicate degree of spermatogenesis. Relative horn size is also indicated, showing casting in early winter. (Data taken from Moy, 1970, and O'Gara et al., 1971).)

amounts, they tend to direct their marking with the subauricular gland toward these objects. Almost all the isolated fractions stimulate marking above that of nonsmeared objects. However, isovaleric acid is far more effective than any other constituent, suggesting that it is the primary pheromone involved in territorial behaviors.

Gilbert (1974) has recently provided details on the social behavior of the pronghorn living in Yellowstone National Park. During the winter the sexes live in mixed groups, but beginning in March the aggregations break down and the mature males establish territories which are occupied through the summer and the breeding season. The onset of territoriality corresponds to testicular growth and spermatogenesis.

Immature males less than 3 years old form bachelor herds in which a dominance hierarchy is established. These males occupy inferior habitats adjacent to territories. While bachelors commonly court estrous females, they rarely mate. Dominant males also court and mount subordinate males. All bachelor males attempt to invade territories occupied by mature males.

The territorial males do a great deal of marking with the subauricular gland, rubbing the gland on bushes and grasses, especially along the borders of the territories. A male will periodically go on "marking patrols," in which marking is intense and prolonged. Often this is associated with other activities that distinguish the territory, such as sniffing, pawing the ground, urinating, and defecating. Frequently these marking activities precede the courting of females, suggesting that they stimulate sexual behaviors. Marking patrols are often synchronized among different males. For seven patrols involving three males, the onsets were synchronized within 25 minutes. Perhaps this is not too surprising, since marking predominates in the late afternoon and may be stimulated by declining light or temperature.

Scent deposition does not prevent intrusion of a territory by an interloper, a finding common to all scent-marking mammals. It may, however, increase a territorial male's confidence and increase the likelihood of victory. Marking occurs during direct encounters between territorial males, suggesting an intimidation function. It could also function to hold females to familiar-smelling territories and increase their sexual receptivity.

Bucks with females during the rut spend up to 60% of their time staring into the distance and guarding against intrusion. Among territories in which there is a cul-de-sac, the vigilance is directed almost entirely toward the only possible approach by other males. Characteristically the male will herd his females deep into the territory out of sight of intruders and then interpose himself between the females and the potential invaders.

It seems rather odd that males establish territories and breeding herds months before the rut, but it may be necessary in order to protect the females during a period when nutritive preparation for mating is occurring. Unlike territorial males, bachelor males will pursue females unremittingly. Without a territorial sanctuary, the female could go into negative energy balance and be unfit for mating and maternal responsibilities. Finally, living in a territory prevents food competition between bachelors and nursery herds.

Overall the pronghorn is ideally adapted for territorial responses, showing a tight covariation between physiological and morphological determinants of mating ability, scent marking, territorial defense, and mating behaviors. The social organization assures that females are protected and mated by males capable of holding territories and commanding foraging areas. The society is synchronized by photoperiods and possibly temperature changes, allowing births to occur in the spring, when offspring have the best chance of survival.

Black-Tailed Deer (Odocoileus hemionus)

This beautiful deer is distributed along the Pacific coast of North America from northern California to British Columbia. Although little is known about its social behavior, especially in regard to olfactory signaling, it is known to be periodically active during the day and night, highly gregarious, and dependent on scent communication (Müller-Schwarze & Müller-Schwarze, 1969). The deer rely on four major scent gland complexes: (a) preorbital glands immediately anterior to the eye, (b) tarsal glands on the inner side of the tarsal joints, (c) metatarsal glands on the outside of the hind foot, and (d) interdigital glands located between the toes of all four feet. In addition, the dorsal and lateral areas around the tails of males contain moderately enlarged sudoriferous and sebaceous glands. The preorbital glands are poorly developed and are used infrequently, whereas the tarsal and metatarsal glands are highly developed and extensively used. The interdigital glands, used in trail marking, have not been investigated in detail.

The most extensively studied scent gland is the tarsal gland (Müller-Schwarze, 1971). It is composed of enlarged sebaceous and sudoriferous (sweat) tissue, along with erector piliform muscles. The gland stimulates investigations by conspecifics and is used for individual recognition: There is a baseline level of investigation of about once per hour per individual in an established group. This investigation increases to approximately 11 per hour when a strange female is introduced to the group, and is at least twice this frequent if the intruder is a male. Most often the tarsal gland of the newcomer is avidly investigated, while the newcomer is usually not permitted to reciprocate. Sniffing occurs much more often in the dark, suggesting the enhanced importance of olfactory communication when vision is precluded.

When bucks threaten each other, they spread the hair turfs on the gland and expose the scent tissue. They also spray scent by rubbing the tarsal glands together while urinating on them. Males and females of all ages will occasionally urine rub the tarsal glands. The urine is usually licked off the tarsal hair afterward. The posture is quite different from that for evacuation urinating; in males the urine is repeatedly released in smaller amounts as part of his display.

When the material from the tarsal turf is rubbed on a male or female tarsal joint, other animals approach, sniff, and lick the material. If the material is applied on another area, air sniffing is stimulated but the animals fail to locate the source. Apparently background odors are important, since the tarsal gland material from a male is up to 10 times as effective in stimulating female interest when it is applied to the male rather than to the female.

The effective material can be extracted from the gland with petroleum ether or methylene chloride. The distillate of the extract will elicit the typical investigatory response. Gas–liquid chromatography has led to the fractionation of dozens of compounds from the tarsal gland extract (Müller-Schwarze, 1969a, 1971). The chief component with behavioral effects has been identified as *cis*-4-hydroxydodec-6-enoic acid lactone, although the inclusion of more components increases the response intensity. Interestingly, other related unsaturated lactones are active, but not saturated compounds. The number of carbon atoms present is less important than the double bonding. These differences indicate specificity of the lactone molecule in olfactory communication.

Scent signaling occurs with other gland complexes as well. The metatarsal gland responds in fear-provoking situations, such as when the animals encounter a dog or are released into a strange environment. Conspecific reactions to metatarsal secretion are difficult to evaluate because when alarmed, the deer respond with many reactions (erected tail and anal hair, hissing, stamping, etc.). No chemical identification has been attempted, although the odor has been likened to garlic.

Forehead rubbing has also been observed. It occurs on branches and other objects, especially close to the sleeping areas. A twig marked in this way by one individual becomes the object of attention for others of the group. When a male or female enters a strange group, the initial activity is sniffing of the dry tips of bushes and low tree branches. Obviously an olfactory signal is being used, probably serving territorial functions. Again no attempt has been made to identify the secretory material.

Müller-Schwarze and Müller-Schwarze (1975) have recently compared subspecies of *Odocoileus* for their reactions to each other's tarsal scent signals. The black-tailed deer (*O. hemionus columbianus*) and the Rocky Mountain mule deer (*O. hemionus hemionus*) share a common range in the northwest United States. It is possible that tarsal recognition signals have diversified under pressures of sympatric living, although hybridization has been described.

Experiments with tarsal gland extracts indicated that the black-tailed deer responded more strongly toward tarsal gland extracts of their own subspecies than to those from the mule deer. Similarly, the mule deer showed greater interest in their own olfactory material. Thus, the tarsal odor can serve as a social and sexual barrier between the two subspecies.

Research with the black-tailed deer has been highly rewarding. Observations by Müller-Schwarze and his associates have provided insights into the communication among cervids and extended our knowledge of adaptive behaviors and olfactory signals. Much more work is needed, however, to tie these observations to reproductive fitness. Clearly other cervids will have to be studied in equal detail, as the observations on the black-tailed deer only illustrate species specificity. As indicated above, the black-tailed deer has a poorly developed preorbital gland, whereas many other cervids have highly active glands. The caribou (*Rangifer caribou*), for example, produces a strong odor from this gland. More pronounced tail glands appear in the red deer (*Cervus elaphus*) and musk deer (*Moschus moschuferus*). The latter species marks branches of trees with this gland. Forehead rubbing appears in the black-tailed deer and also in the male roe deer (*Capreolus capreolus*), in which the forehead gland is enlarged and shows a variation in size according to the season. The differences, such as these, may relate to specific adaptations of ecological and social variables.

Maxwell Duiker (Cephalophus maxwelli)

The Maxwell duiker is a small antelope living in the forests of West Africa. Like many of its Bovidae relatives it possesses an enlarged maxillary gland anterior to the orbit, which it uses to mark objects and conspecifics. The gland characteristics have not been described, although it is likely that it is composed of active sebaceous and apocrine tissue. Almost nothing is known about the duiker's style of life, although recent studies on captive animals suggest that it possesses many of the responses typical of ungulates (Ralls, 1971). It was one of the first animals observed to scent mark with the preorbital gland

(Aeschlimann, 1963; Ogilby, 1836, cited by Pocock, 1910; Rahm, 1960).

In accordance with observations on most mammals, males mark objects and each other more frequently than do females, dominant males mark more than subordinate males, and marking is stimulated by agonistic encounters. Preorbital scent marking may also be associated with individual recognition or social appeasement, as male and female will often face each other and press their glands together, first on one side of the face and then on the other.

Ralls (1971) distinguished two types of females: Type A, which frequently scent grooms males, and Type B, which does not. While Type A females are not necessarily dominant over Type B females, they do mark much more frequently in all situations. Apparently these frequently marking individuals have achieved a closer relationship with the males and may enjoy a privileged mating status. The introduction of a stranger into an established group evokes extremely high levels of preorbital marking, remindful once again of most mammals. Interestingly, the increase in marking is only evident in homosexual encounters, indicating that sex recognition is possible and that this recognition modulates marking activities. These relationships are seen in Table 7. The Maxwell duiker would be an interesting species for further studies, as it is small, exists well in captivity, and seems to have a behavioral repertoire common to many ungulates. Its enlarged orbital gland, associated with high levels of scent marking, presents ideal conditions for the biochemical analysis of olfactory signals.

Lemur Monkey (Lemur catta *and* Propithecus verrauxi)

The scent-marking behavior of two species of arboreal lemur monkeys, *Propithecus verrauxi* and *Lemur catta,* has been studied in detail by Jolly (1966). Both species are found on the island of Madagascar, having overlapping niches in which they share the same food supplies and territories. In fact, members of both species can often be found in the same tree. *P. verrauxi* has a smaller troop size (around 3–4 animals) than *L. catta* (10–12 animals). Both have well-defined territories, although in *P. verrauxi* there is no dominance in the troop unless the female is in estrus, while among troops of *L. catta* there is a clear dominance order among the males and a looser one among females, with females dominant over males. In both species the female breeds only once a year and the majority, if not all, of the aggressive encounters within a troop occur in the time immediately preceding and during the period of the females' receptivity.

TABLE 7

Sex and Social Determinants of Preorbital Scent Marking in the Maxwell Duiker

Subject	Social status	Marking activity in own groups	Marking activity after introduction of male or female	
			Male	Female
Males				
	1	6.6	15.2	6.1
	2	5.8	10.7	6.2
	3	4.4	8.6	4.1
Type A females (high markers)				
	1	3.5	3.7	18.6
	2	3.4	3.1	12.2
	3	1.5	0.0	1.7
Type B females (low markers)				
	1	0.1	0.0	0.1
	2	0.0	0.1	0.0
	3	0.0	0.0	0.0

Note. Data taken from Ralls (1971).

P. verrauxi has four means of depositing odors in the environment, with a throat gland, genital secretions, and urine and fecal matter. The throat area has a long dark gland down its ventral surface, and this area is rubbed on trees in a stereotyped fashion (Jolly, 1966). Other troop members sniff these marked areas frequently and often re-mark them with their throat glands or urine. Urine marking is more common than marking with the throat gland and is also performed in a stereotyped manner. It is seen more often in males than in females.

Male and female *L. catta* deposit secretions from the genitalia by rubbing them on branches. Females show a peak of genital marking during estrus. Males have three additional sources of odors, the palmar, brachial, and antebrachial glands. The brachial gland is about 2 cm in diameter and consists mainly of sebaceous tissue. The antebrachial gland associated with the spur on the inner forearm contains apocrine and eccrine tissues along with cells that resemble the interstitial cells of the testis. The behaviors involved in the deposition of odoriferous material from these glandular areas are often complex and have a very large visual component. When a male marks with the palmar gland, he typically stands on his hind legs, grabs a twig or branch with both hands, and jerks his shoulders from side to side pulling his hands around the branch and depositing material from the glands. The odors from the brachial and antebrachial glands are combined when the animal touches his forearm to the brachial area. Following this, he brings his tail forward between his legs and pulls it up and down several times so that the combined gland odors are deposited on his tail. These odors are then spread by means of a display in which the animal stands on all fours with his tail arched and quivering violently over his back. Tail waving is always directed toward another animal. A characteristic of the *L. catta* is a complex series of behaviors, termed a "stink fight" by Jolly (1966), which involves a series of palmar marking, tail marking, and tail waving directed by two males toward each other.

If these two species may be considered representative of lemur monkeys, marking in lemurs is often triggered by the onset of the female's estrous period. The behaviors making up a stink fight in *L. catta* may be under the control of sex hormones since they occur only in males who are beyond puberty. However, there is essentially no specific information on the hormone or brain control mechanisms involved. This group of monkeys, particularly *L. catta,* would provide an excellent system for more research into the coordination of visual and olfactory signals in primates.

Marmoset Monkey (Callithrix jacchus, Laguinus fuscicollis, *and* Leontideus rosalia)

Although little general information is available regarding the relationship between scent marking and the ecology of the marmoset monkey, Epple (1973) has extensively studied the marking behavior and responses to odors in two species of marmoset: the common marmoset (*Callithrix jacchus*) and the saddle-backed tamarin (*Laguinus fuscicollis*). *L. fuscicollis* has large scent glands in the circumgenital, suprapubic, and sternal areas, and deposits secretions when these areas are rubbed against objects in the environment and on conspecifics (Epple, 1974a, 1974b). *C. jacchus* also rubs its circumgenital area against items in the environment, and the secretions of the apocrine and sebaceous glands covering the genital and circumgenital area, as well as drops of urine, are mixed, leaving a thin film on objects (Epple, 1970).

When a group of *C. jacchus* is presented with a clean perch, it is scent marked, mostly by the dominant animal. If the perch has been previously marked by other animals, even more marking is elicited (Epple, 1970). When grouped monkeys are presented with a choice of two perches, they show preferences for one of them, as indicated by increased sniffing and scent marking of the preferred perch. Perches previously marked by a strange male are preferred over perches marked by a strange female, indicating that the marks carry information about the sex of the donor. Epple (1974a, 1974b) suggested that this preference is due to qualitative rather than quantitative differences in the odor. Grouped *L. fuscicollis* also preferred perches marked by a stranger with whom they had recently had an aggressive encounter over those marked by a "neutral" stranger of the same sex. These preferences were found not only immediately after the encounter but also 3 days later (Epple, 1973), indicating that odor from scent marks may carry long-term information for individual identification. In both of the above cases, no preference was shown for perches marked only with urine. The animals also show preferences for perches marked by a dominant rather than a submissive animal (male or female), but these preferences may be a result of quantitative differences in sebum intensity, since dominant animals tend to mark more often than submissive animals (Epple, 1974a, 1974b).

Marmosets increase the frequency of scent marking both before and after copulation (Epple, 1974b). *C. jacchus* have independent rank orders for males and females, and the dominant animal of both sexes scent marks more often than subordinates. When a group of *C. jacchus* is exposed to a strange animal, the dominant animal of the same sex as the stranger (Epple, 1970) typically attacks the stranger and increases its frequency of scent marking. Lion marmosets (*Leontopithecus rosalia*) housed in open-air enclosures show increased scent marking after heavy rainfalls (Snyder, 1972). These examples imply that scent marking in marmosets is related to sex behavior, aggression, and possibly homesite odors. The control of scent marking in these species is interesting because dominant males and females scent mark frequently, yet there may be separate hormonal control mechanisms for each sex. Unfortunately, no information is available regarding castration or hormone replacement effects. The clear preferences shown by these animals for odors from other animals may provide a system for identification of the olfactory component involved, although if marmosets can be individually recognized on the basis of odor, chemical pheromones may be quite complex.

General Characteristics of Scent-Marking Species

Reference to Table 8 indicates several features of scent-marking behavior in mammals. In almost all cases studied, marking is sexually dimorphic, with the male engaging in this behavior more frequently than the female. Females may mark more frequently during selected periods of their reproductive cycle, but information is generally lacking. Typically, marking behavior is displayed postpuberally and is correlated with seasonal variations in reproduction. Marking frequency is positively related to dominance and is most evident during aggressive encounters. Limited observations also suggest that sexual encounters are either preceded or followed by increased marking.

Sexual dimorphism, age dependency, seasonal variations, and in some cases, direct observations of hormone status suggest that gonadal hormones (especially androgens and estrogens) control the frequency of response

TABLE 8

General Characteristics of Scent Gland Marking in Various Mammalian Species

Characteristics of marking	Ground squirrel	Mongolian gerbil	Golden hamster	Guinea pig	North American pika	Sugar glider	European rabbit	Pronghorn antelope	Black-tailed deer	Maxwell duiker	Lemur monkey	Marmoset monkey
Sexually dimorphic	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes	?
Age dependent	Yes	Yes	Probably	Yes	?	Probably	Probably	?	?	?	Probably	Probably
Seasonal development	Yes	Probably	?	?	Yes	?	Yes	Yes	Yes	?	Yes	?
Circadian	?	Probably	?	?	?	?	?	Yes	?	?	?	?
Dominance related	Yes	Yes	Yes	Yes	Probably	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Stimulated by aggression	Yes	Yes	Yes	Yes	?	Probably	Yes	Yes	Yes	Yes	Probably	Yes
Stimulated by sex	?	Probably	Yes	?	?	?	Probably	Yes	?	Probably	Probably	Yes
Androgen dependent in male	Probably	Yes	Yes	Probably	?	?	Yes	Probably	?	?	Probably	?

Note. ? = data indeterminate.

in nearly all mammalian species. This is not surprising, as the chemosignals that relate to dominance status and reproductive capacities are necessarily tied to the same hormonal system: Evolution has capitalized on endocrine activities to integrate related functions. In the broadest sense, then, scent marking is a reproductive activity.

Almost no neurophysiological work has been done with scent marking. In the case of the Mongolian gerbil, however, the preoptic brain area has been implicated. This central area has been demonstrated to influence sex behavior in several mammalian species, again suggesting common processes. A great lack of information lies in the central control of marking. Other problem areas need additional investigation. Table 8 points to some of the gaps in our knowledge. Until similar behavioral features are studied in a number of species, it is impossible to make detailed comparative statements. Similarly, scent-marking pheromones have been identified in only three or possibly four species: the Mongolian gerbil, European rabbit, black-tailed deer, and pronghorn antelope. Unlike hormones, pheromone composition between species appears variable, even though the function may be similar. Again, more information is needed before anything general can be said.

It is interesting to note that scent marking within territories rarely deters invasions by members of other populations. In fact, there appears to be no evidence that olfactory signals create impenetrable barriers of any kind. Of course the chemicals can communicate numerous things (Table 1) and need not be directly related to territoriality. Some animals do post scent cues at the periphery of territories and increase their marking during territorial disputes, strongly suggesting a territorial function. The opinion is growing that the territorial signals do not exclude intrusions but rather offer "security" to territorial holders and "intimidate" invaders. There is only one clear demonstration that scent marks bias the outcome of agonistic encounters (Mykytowycz, 1974), but the effect could be more general. Certainly, it is reasonable to assume that territorial signals should be constantly tested for their validity by potentially more adaptive individuals. Current studies suggest that motivational functions modulate and direct scent communication. Scent marking is not stereotyped and mechanistic; it is variable and goal-directed. The functions, therefore, cannot be described entirely on the behavioral level and cannot be predicted solely in terms of genetic mechanisms. One must be willing, at this point in time, to postulate motivational mechanisms and drive systems. These, then, are amenable to the usual physiological attacks that have been successful in other fields of behavior. Analyses of scent marking require a detailed description of behaviors within, as well as outside, the laboratory. Related to this is a need to specify the psychophysical relations between olfactory stimuli and behavioral components.

Finally, it should be noted that laboratory studies stand at the fulcrum between ethological investigations of field behavior and biochemical investigations of physiological mechanisms. Whereas it is extremely difficult to tie naturalistic behavior to biochemical processes, it is less difficult to link field observations and biochemical findings to laboratory studies of behavior. Behavioral laboratory data can be validated against the diverse views gained from the field and from cellular manipulations.

REFERENCE NOTES

1. Steiner, A. Personal communication, May 1975.
2. Nichol, A. A. *Experimental feeding of deer* (Tech. Bull. 75). Tucson: University of Arizona, Agricultural Experimental Station, 1938.
3. Murphy, M. R. *Olfactory bulb removal reduces social territorial behavior in the male golden hamster.* Paper presented at the meeting of the Eastern Psychological Association, Atlantic City, New Jersey, April 1970.
4. Johnston, R. E. *Scent marking in female hamsters.* Paper presented at the Eastern Psychological Association, Atlantic City, New Jersey, 1970.
5. Sharp, P. L. *Behavior of the pika* (Ochotona princeps) *in the Kananaskis region of Alberta.* Unpublished master's thesis, University of Alberta, Edmonton, Canada, 1973.

REFERENCES

Aeschlimann, A. Observations sur Philantomba maxwelli (Hamilton-Smith) une antilope de la forêt eburnée. *Acta Tropica,* 1963, *20,* 341–368.

Alberts, J. R., & Friedman, M. I. Olfactory bulb removal but not anosmia increases emotionality and mouse killing. *Nature,* 1972, *238,* 454–455.

Andrew, R. J. The displays of the primates. In J. Buettner-Janusch (Ed.), *Evolutionary and genetic biology of primates* (2 vols.). New York: Academic Press, 1964.

Bailey, V. *The mammals and life zones of Oregon* (North American Fauna 55, U.S. Department of Agriculture). Washington, D.C.: U.S. Government Printing Office, 1936.

Bandler, R. J., & Chi, C. C. Effects of olfactory bulb removal on aggression: A reevaluation. *Physiology and Behavior,* 1972, *8,* 207–212.

Baran, D. Responses of male Mongolian gerbils to male gerbil odors. *Journal of Comparative and Physiological Psychology,* 1973, *84,* 63–72.

Baran, D., & Glickman, S. E. Territorial marking in the Mongolian gerbil: A study of sensory control and function. *Journal of Comparative and Physiological Psychology,* 1970, *71,* 237–245.

Barash, D. P. Territorial and foraging behavior of Pika (*Ochotona princeps*) in Montana. *American Midland Naturalist,* 1973, *89,* 202–207.

Beach, F. A. Effects of gonadal hormones on urinary behavior in dogs. *Physiology and Behavior,* 1974, *12,* 1005–1014.

Beauchamp, G. K. Perineal scent gland and social dominance in the male guinea pig. *Physiology and Behavior,* 1974, *13,* 669–673.

Beruter, J., Beauchamp, G. K., & Muetterties, E. L. Mammalian chemical communication: Perineal gland secretion of the guinea pig. *Physiological Zoology,* in press.

Bethe, A. Vernachlassigte hormone. *Naturwissenschaften,* 1932, *20,* 177–181.

Birch, M. C. (Ed.). *Pheromones.* Amsterdam: North Holland Publishing, 1974.

Blum, M. S. Pheromonal bases of social manifestations in insects. In M. C. Birch (Ed.), *Pheromones.* Amsterdam: North Holland Publishing, 1974.

Broadbooks, H. E. Ecology and distribution of the pikas of Washington and Alaska. *American Naturalist,* 1965, *73,* 299–336.

Bronson, F. H. Rodent pheromones. *Biology of Reproduction,* 1971, *4,* 344–357.

Bronson, F. H. Pheromonal influences on reproductive activities in rodents. In M. E. Birch (Ed.), *Pheromones.* Amsterdam: North Holland Publishing, 1974.

Brown, L. E. Home range and movement of small mammals. *Symposium of the Zoological Society of London,* 1966, *18,* 111–142.

Brown, W. L. An hypothesis concerning the function of the metapleural glands in ants. *American Naturalist,* 1968, *102,* 188–191.

Brownlee, R. G., Silverstein, R. M., Müller-Schwarze, D., & Singer, A. G. Isolation, identification and function of the chief component of the male tarsal scent in black-tailed deer. *Nature,* 1969, *221,* 284–285.

Butler, C. G. Chemical communication in insects: Behavioral and ecologic aspects. In J. W. Johnston & D. G. Moulton (Eds.), *Communication by chemical signals.* New York: Appleton-Century-Crofts, 1970.

Butler, C. G., Callow, R. K., & Johnston, N. C. The isolation and synthesis of queen substance, 9-oxodec-trans-2-enoic acid, a honeybee pheromone. *Proceedings of the Royal Society of Britain,* 1961, *155,* 417–432.

Cheal, M. L., & Sprott, R. L. Social olfaction: A review of the role of olfaction in a variety of animal behaviors. *Psychological Reports,* 1971, *29,* 195–243.

Desjardins, C., Maruniak, J. A., & Bronson, F. H. Social rank in house mice: Differentiation revealed by ultraviolet visualization of urinary marking patterns. *Science,* 1973, *182,* 939–941.

Devor, M., & Murphy, M. R. The effect of peripheral olfactory blockade on the social behavior of the male golden hamster. *Behavioral Biology,* 1973, *9,* 31–42.

Dieterlen, F. *Das Verhalten des syrischen Goldenhamsters* (*Mesocricetus auratus Waterhouse*)*: Untersuchungen zur Frage seiner Entwicklung und seiner angeborener Anteil durch geruchsisolierte Aufzuchten. Zeitschrift für Tierpsychologie,* 1959, *16,* 47–103.

Drickamer, L. C., Vandenbergh, J. G., & Colby, D. R. Predictors of dominance in the male golden hamster (*Mesocricetus auratus*). *Animal Behaviour,* 1973, *21,* 557–563. (a)

Drickamer, L. C., Vandenbergh, J. G., & Colby, D. R. Predictors of social dominance in the adult female golden hamster (*Mesocricetus auratus*). *Animal Behaviour,* 1973, *21,* 564–570. (b)

Dücker, G. Das Verhalten der Viverriden. In W. G. Kükenthal, *Handbuch der Zoologie; eine Naturgeschichte der Stämme des Tierreiches* (Vol. 81). Berlin: W. de Gruyter, 1965.

Edwards, D. A., Thompson, M. L., & Burge, K. G. Olfactory bulb removal vs. peripherally induced anosmia: Differential effects on the aggressive behavior of male mice. *Behavioral Biology,* 1972, *7,* 823–829.

Eibl-Eibesfeldt, I. *Eine besondere Form des Duftmarkierns beim Riesengalago Galago crassicaudatus. Säugetierkundliche Mitteilungen,* 1953, *1,* 171–173. (a)

Eibl-Eibesfeldt, I. *Ethologische Unterschiede zwischen Hausratte und Wanderrate. Zoologischer Anzeiger Supplement,* 1953, *16,* 169–180. (b)

Eibl-Eibesfeldt, I. *Vergleichende Studien an Ratten and Mausen Prakt. Desinfektor,* 1953, *45,* 166–168. (c)

Eibl-Eibesfeldt, I. *Zur Ethologie des Hamsters* (*Cricetus cricetus L.*). *Zeitschrift für Tierpsychologie,* 1953, *10,* 204–254. (d)

Eisenberg, J. F. A comparative study in sandbathing behavior in heteromyid rodents. *Behaviour,* 1963, *22,* 16–23.

Eisenberg, J. F. A comparative study in rodent ethology with emphasis on evolution of social behavior, I. *Proceedings of the U.S. National Museum,* 1967, *122,* 1–51.

Eisenberg, J. F., & Kleiman, D. G. Olfactory communication in mammals. In *Annual Review of Ecology and Systematics,* 1972, *3,* 1–32.

Eisenberg, J. F., & Kuehn, R. E. The behavior of *Ateles geoffroyi* and related species. *Smithsonian Miscellaneous Collection,* 1966, *151,* 4683.

Epple, G. Comparative investigation on sexual and social behavior of Hapalidae. *Folia Primatologica,* 1967, *7,* 37–65.

Epple, G. Quantitative studies on scent marking in the marmoset (*Callithrix jacchus*). *Folia Primatologica,* 1970, *13,* 48–62.

Epple, G. The role of pheromones in the social communication of marmoset monkeys (Callithricidae). *Journal of Reproduction and Fertility* (Supplement), 1973, *19,* 447–454.

Epple, G. Olfactory communication in South American primates. *Annals of the New York Academy of Sciences,* 1974, *237,* 261–278. (a)

Epple, G. Primate pheromones. In M. C. Birch (Ed.), *Pheromones.* Amsterdam: North Holland Publishing, 1974. (b)

Epple, G., & Lorenz, R. Distribution, morphology and function of the sternal glands in the platyrrhini. *Folia Primatologica,* 1967, *7,* 98–126.

Ewer, R. F. *Ethology of mammals.* New York: Plenum Press, 1968.

Fradrich, H. The behavior of swine (Suidae, Tayassuidae) and hippopotami (Hippopotamidae). *Handbook of Zoology,* 1967, *8,* 42.

Frank, F. Das Duftmarkieren der grossen Wuhlmaus, *Arvicola terrestris (L.) Säugetierkundliche Mitteilungen,* 1956, *21,* 172–175.

Gary, N. E. Pheromones that affect the behavior and physiology of honey bees. In M. C. Birch (Ed.), *Pheromones.* Amsterdam: North Holland Publishing, 1974.

Geist, V. On the relationship of social evolution and ecology in ungulates. *American Zoologist,* 1974, *14,* 205–220.

Gilbert, B. K. Scent marking and territoriality in pronghorn (*Antilocapra americana*) in Yellowstone National Park. *Mammalia,* 1974, *37,* 25–33.

Gleason, K. K., & Reynierse, J. H. The behavioral significance of pheromones in vertebrates. *Psychological Bulletin,* 1969, *71,* 58–73.

Goodrich, B. S., & Mykytowycz, R. Individual and sex differences in the chemical composition of pheromone-like substances from the skin glands of the rabbit, *Oryctolagus cuniculus. Journal of Mammalogy,* 1972, *53,* 540–548.

Halpin, Z. T. Individual differences in the biological odors of the Mongolian gerbil (*Meriones unguiculatus*). *Behavioral Biology,* 1974, *11,* 253–259.

Hart, B. L. Environmental and hormonal influences on urine marking behavior in the adult male dog. *Behavioral Biology,* 1974, *11,* 167–176. (a)

Hart, B. L. Gonadal androgen and sociosexual behavior of male mammals: A comparative analysis. *Psychological Bulletin,* 1974, *81,* 383–400. (b)

Harvey, E. B., & Rosenberg, L. E. An apocrine gland complex of the Pika. *Journal of Mammalogy,* 1960, *41,* 213–219.

Hediger, H. Saugetier-Territorien und ihre Markierung. *Bijdragen tot de Dierkde,* 1949, *28,* 172–184.

Hesterman, B., & Mykytowycz, R. Some observations on the odours of anal gland secretions from the rabbit, *Oryctolagus cuniculus (L). CSIRO Wildlife Research,* 1968, *13,* 71–81.

Hill, W. C. O. Behavior and adaptation of the primates. *Proceedings of the Royal Society of London,* 1956, *66,* 94–110. (a)

Hill, W. C. O. Body odor in lorises. *Proceedings of the Zoological Society of London,* 1956, *127,* 580. (b)

Howell, A. B. Habits of the three subgenera studied. In, *Anatomy of the wood rat.* Baltimore: Williams & Wilkins, 1926.

Johnson, R. P. Scent marking in mammals. *Animal Behaviour,* 1973, *21,* 521–535.

Johnston, J. W., Moulton, D. G., & Turk, A. (Eds.), *Advances in chemoreception.* New York: Appleton-Century-Crofts, 1970.

Johnston, R. E. Sex pheromones of the golden hamster. *American Zoologist,* 1972, *12,* 662.

Johnston, R. E. Sexual attraction function of golden hamster vaginal secretion. *Behavioral Biology,* 1974, *12,* 111–117.

Johnston, R. E. Scent marking by male golden hamsters (*Mesocricetus auratus*) I. Effects of odors and social encounters. *Zeitschrift für Tierpsychologie,* in press. (a)

Johnston, R. E. Scent marking in male hamsters II. The role of the flank gland scent in the causation of marking. *Zeitschrift für Tierpsychologie,* in press. (b)

Johnston, R. E. Scent marking by male golden hamsters (*Mesocricetus auratus*) III. Behavior in a semi-natural environment. *Zeitschrift für Tierpsychologie,* in press. (c)

Jolly, A. *Lemur behavior: A Madagascar field study.* Chicago: University of Chicago Press, 1966.

Karlson, P., & Butenandt, A. Pheromones (ectohormones) in insects. *Annual Review of Entomology,* 1959, *4,* 39–58.

Kaufmann, J. H. A three-year study of mating behavior in a free-ranging band of rhesus monkeys. *Ecology,* 1965, *30,* 146–155.

King, J. A. Social behavior and population dynamics of the black-tailed prairie dog. *Contributions in Laboratory Vertebrate Biology* (University of Michigan), 1955, *67,* 1–123.

Kivett, V. K. *Variations in integumentary gland activity and scent marking in columbian ground squirrels* (Spermophilus c. columbianus). Unpublished doctoral dissertation, University of Alberta, 1975.

Kleiman, D. G. Scent marking in the Binturong, *Arctictis Binturong. Journal of Mammalogy,* 1974, *55,* 224–227.

Kramer, A. Social organization and social behavior in chamois population (*Rupicapra rupicapra L*) of the Alps. *Zeitschrift für Tierpsychologie,* 1970, *26,* 889–964.

Kuhme, W. Beobachtungen am Afrikanischen Elefanten (*Loxodonta africana Blumenbach,* 1797) in Gefangenschaft. *Zeitschrift für Tierpsychologie,* 1961, *18,* 285–296.

Kunkel, P., & Kunkel, I. Beitrage zur Ethologie des Hausmeerschweinchens *Cavia aperea f. porcellus (L). Zeitschrift für Tierpsychologie,* 1964, *21,* 602–641.

Linsdale, J. M. *The California ground squirrel: A record of observations made on the Hastings Natural History Reservation.* Berkeley: University of California Press, 1946.

Linsdale, J. M., & Levis, L. P. *The dusky-footed wood rat: A record of observations made on the Hastings Natural History Reservation.* Berkeley: University of California Press, 1951.

Lipkow, J. Uber des Seitenorgan des Goldhamsters (*Mesocricetus auratus Waterhouse*). *Zeitschrift für Morphologie und Oekologie de Tiere,* 1954, *42,* 333–372.

Markham, O. D., & Whicker, F. W. Seasonal data on reproduction and body weight of pikas (*Ochotona princeps*). *Journal of Mammalogy,* 1973, *54,* 496–498.

Marsden, H. M., & Holler, N. R. Social behavior in confined populations of the cottontail and the swamp rabbit. *Wildlife Monographs of Chestertown,* 1964, *13,* 6–39.

Martan, J. Effect of castration and androgen replacement on the supracaudal gland of the male guinea pig. *Journal of Morphology,* 1962, *110,* 285–298.

Martan, J., & Price, D. Comparative responsiveness of supracaudal and other sebaceous glands in male and female guinea pigs to hormones. *Journal of Morphology,* 1967, *121,* 209–222.

Mason, W. A. Social organization of the South American monkey, *Callicebus moloch:* A preliminary report. *Tulane Studies in Zoology,* 1966, *13,* 23–28.

McClintock, M. K. Menstrual synchrony and suppression. *Nature,* 1971, *229,* 244–245.

Millar, J. S. Adrenal weights in relation to reproductive status in the pika, *Ochotona princeps* (Richardson). *Canadian Journal of Zoology,* 1970, *48,* 1137–1140.

Moy, R. F. Histology of the subauricular and rump glands of the pronghorn (*Antilocapra americana Ord*). *American Journal of Anatomy,* 1970, *129,* 65–88.

Moynihan, M. Communication in Callicebus. *Journal of Zoology, London,* 1966, *150,* 77–127.

Moynihan, M. Comparative aspects of communication in New World Primates. In D. Morris (Ed.), *Primate ethology.* Chicago: Aldine Press, 1967.

Müller-Schwarze, D. Social odors in young male deer. *American Zoologist,* 1967, *7,* 430.

Müller-Schwarze, D. Complexity and relative specificity in a mammalian pheromone. *Nature,* 1969, *223,* 525–526. (a)

Müller-Schwarze, D. Pheromone function of deer urine. *American Zoologist,* 1969, *9*(3)A. (b)

Müller-Schwarze, D. Pheromones in black-tailed deer (*Odocoileus hemionus columbianus*). *Animal Behaviour,* 1971, *19,* 141–152.

Müller-Schwarze, D., & Müller-Schwarze, C. A herd of black-tail deer. *Pacific Discovery,* 1969, *12,* 22–26.

Müller-Schwarze, D., & Müller-Schwarze, C. Subspecies specificity of response to a mammalian social odor. *Journal of Chemical Ecology,* 1975, *1,* 125–133.

Müller-Schwarze, D., Müller-Schwarze, C., Singer, A. G., & Silverstein, R. M. Mammalian pheromone: Identification of active component in the subauricular scent of the male pronghorn. *Science,* 1974, *183,* 860–862.

Murphy, M. R. Territorial behavior of the caged golden hamster. *Proceedings of the 78th Annual Convention of the American Psychological Association,* 1970, *5,* 237–238. (Summary)

Murphy, M. R. Effects of female hamster vaginal discharge on the behavior of male hamsters. *Behavioral Biology,* 1973, *9,* 367–377.

Muul, I. Day length and food caches. In *Field studies in natural history* (articles from *Natural History*). New York: Van Nostrand Reinhold, 1970.

Myers, K., & Poole, W. E. A study of the biology of the wild rabbit, *Orytolagus cuniculus* (*L*), in confined populations. The effects of season and population increase on behavior. *CSIRO Wildlife Research,* 1961, *6,* 1–41.

Mykytowycz, R. Further observations on the territorial function and histology of the submandibular cutaneous (chin) glands in the rabbit, *Oryctolagus cuniculus (L). Animal Behaviour,* 1965, *8,* 400–411.

Mykytowycz, R. Observations on odoriferous and other glands in the Australian wild rabbit, *Oryctolagus cuniculus* (*L*), and the hare, *Lepus europaeus P.* I. The anal gland. *CSIRO Wildlife Research,* 1966, *11,* 11–29. (a)

Mykytowycz, R. Observations on odoriferous and other glands in the Australian wild rabbit, *Oryctolagus cuniculus* (*L*), and the hare, *Lepus europaeus P.* II. The inguinal glands. *CSIRO Wildlife Research,* 1966, *11,* 29–64. (b)

Mykytowycz, R. Observations on odoriferous and other glands in the Australian wild rabbit, *Oryctolagus cuniculus* (*L*), and the hare, *Lepus europaeus P.* III. Harder's lachrymal and submandibular glands. *CSIRO Wildlife Research,* 1966, *11,* 65–90. (c)

Mykytowycz, R. Territorial marking by rabbits. *Scientific American,* 1968, *218*(5), 116–126.

Mykytowycz, R. The role of skin glands: Mammalian communication. In J. W. Johnston, D. G. Moulton, & A. Turk (Eds.), *Communication by chemical signals.* New York: Appleton-Century-Crofts, 1970.

Mykytowycz, R. The behavioral role of the mammalian skin glands. *Naturwissenschaften,* 1972, *59,* 133–139.

Mykytowycz, R. Reproduction of mammals in relation to environmental odors. *Journal of Reproduction and Fertility* (Supplement), 1973, *19,* 433–446.

Mykytowycz, R. Odor in the spacing behavior of mammals. In M. C. Birch (Ed.), *Pheromones.* Amsterdam: North Holland Publishing, 1974.

Mykytowycz, R., & Dudzinski, M. L. Aggressive and protective behavior of adult rabbits, *Oryctolagus* *cuniculus* (*L*) towards juveniles. *Behavior,* 1972, *43,* 7–120.

Mykytowycz, R., & Gambale, S. The distribution of dung hills and the behavior of free-living wild rabbits, *Oryctolagus cuniculus* (*L*), on them. *Forma et Functio,* 1969, *1,* 333–349.

Mykytowycz, R., & Goodrich, B. S. Skin glands as organs of communication in mammals. *Journal of Investigative Dermatology,* 1974, *62,* 124–131.

Mykytowycz, R., & Hesterman, B. The behavior of captive wild rabbits, *Orytolagus cuniculus* (*L*), in response to strange dung hills. *Forma et Functio,* 1970, *2,* 1–12.

Nyby, J., Thiessen, D. D., & Wallace, P. Social inhibition of territorial marking in the Mongolian gerbil (*Meriones unguiculatus*). *Psychonomic Science,* 1970, *21,* 310–312.

O'Gara, B. W., Moy, R. F., & Bear, G. D. The annual testicular cycle and horn casting in the pronghorn (*Antilocapra americana*). *Journal of Mammalogy,* 1971, *52,* 537–544.

Owen, K., Wallace, P., & Thiessen, D. D. Effects of intracerebral implants of steroid hormones on scent marking in the ovariectomized female gerbil (*Meriones unguiculatus*). *Physiology and Behavior,* 1974, *12,* 310–312.

Parkes, A. S., & Bruce, H. M. Olfactory stimuli in mammalian reproduction. *Science,* 1961, *134,* 1–6.

Peters, R. P., & Mech, L. D. Scent marking in wolves. *American Scientist,* 1975, *63*(6), 628–637.

Petter, J. J. Ecological and behavioral studies of Madagascar lemurs in the field. *Annals of the New York Academy of Sciences,* 1962, *102,* 267–281. (a)

Petter, J. J. Recherches sur l'écologie et l'éthologie des lémuriens malgaches. *Memoires du Museum National d'Histoire Naturelle* (*Serie A, Zoologie*), 1962, *27,* 146. (b)

Petter, J. J. The lemurs of Madagascar. In I. Devore (Ed.), *Primate behavior.* New York: Holt, Rinehart & Winston, 1965.

Petter, J. J., & Petter-Rousseaux, A. *A propos du lémurien Malgache Cheirogaleus trichotis. Mammalia,* 1956, *20,* 46–48.

Petter-Rousseaux, A. Reproductive physiology and behavior of the lemuroides. In J. Buettner-Janusch (Ed.), *Evolutionary and genetic biology of primates* (Vol. 1). New York: Academic Press, 1964.

Pfeiffer, W. The fright reaction of fish. *Biological Review,* 1962, *37,* 495–511.

Pietras, R. J., & Moulton, D. G. Hormonal influences on odor detection in rats: Changes associated with estrous cycle, pseudopregnancy, ovariectomy and administration of testosterone propionate. *Physiology and Behavior,* 1974, *12,* 475–491.

Pocock, R. I. On the specialized cutaneous glands of ruminants. *Proceedings of the Zoological Society of London,* 1910, 840–986.

Prior, R. *The roe deer of Cranborne Chase.* London: Oxford University Press, 1968.

Quay, W. B. Seasonal and sexual differences in the skin gland of the kangaroo rat (*Dipodomys*). *Journal of Mammalogy,* 1953, *34,* 1–14.

Rahm, U. *Territoriumsmarkierung mit der Voraugendruse beim Maxwell duiker* (*Philantomba maxwelli*). *Säugetierkundliche Mitteilungen,* 1960, *8,* 140–142.

Ralls, K. Mammalian scent marking. *Science,* 1971, *171,* 443–449.

Ropartz, P. The relation between olfactory stimulation and aggressive behavior in mice. *Animal Behaviour,* 1968, *16,* 97–100.

Rowe, B. A., & Edwards, D. A. Olfactory bulb removal: Influences on the aggressive behaviors of male mice. *Physiology and Behavior,* 1971, *7,* 889–892.

Schaffer, J. *Die Hautdrusenorgane der Saugetiere.* Berlin: Wien, 1940.

Schaller, G. B. *The deer and the tiger.* Chicago: University of Chicago Press, 1967.

Schultze-Westrum, T. *Innerartliche Verstandigung Durch dufte beim Gleitbeutler Petaurus breviceps papuanus thomas* (*Marsupialis phalangeridae*). *Zeitschrift für Vergleichende Physiologie,* 1965, *50,* 151–220.

Schultze-Westrum, T. Social communication by chemical signals. In C. Pfaffman (Ed.), *Olfaction and taste.* New York: Rockefeller University Press, 1969.

Scott, J. P., & Fuller, J. L. *Genetics and the social behavior of the dog.* Chicago: University of Chicago Press, 1965.

Sebeok, T. A. (Ed.). *Animal communication: Techniques of study and results of research.* Bloomington: Indiana University Press, 1968.

Singer, A. G., Agosta, W. C., O'Connell, R. J., Pfaffmann, C., Bowen, D. V., & Field, F. H. Dimethyl disulfide: An attractant pheromone in hamster vaginal secretion. *Science,* 1976, *191,* 948–950.

Snyder, P. A. Behavior of *Leontopithecus rosalia* (the golden lion marmoset) and related species: A review. In D. D. Bridgewater, (Ed.), *Saving the lion marmoset.* Proceedings of WAPT Golden Lion Marmoset Conference, 1972, 23–49.

Sprankel, H. On the behavior and breeding of *Tupaia glis* (Diard, 1820) in captivity. *Zeitschrift für wissenschaftliche Zoologie,* 1961, *165,* 187–200.

Steiner, A. L. Descriptive study of some basic activities and behavior in *Spermophilus columbianus columbianus* (Ord.) I. Locomotion, body care, feeding, burrowing, curiosity and alarm, reproduction. *Review of Comparative Animals,* 1970, *4,* 3–21. (a)

Steiner, A. L. Descriptive study of some basic activities and behavior in *Spermophilus columbianus columbianus* (Ord.) II. Group life. *Review of Comparative Animals,* 1970, *4,* 23–42. (b)

Steiner, A. L. Self- and allo-grooming behavior in some ground squirrels (*Sciuridae*), a descriptive study. *Canadian Journal of Zoology,* 1973, *51,* 151–161.

Steiner, A. L. Body-rubbing, marking and other scent-related behavior in some ground squirrels (*Sciuridae*), a descriptive study. *Canadian Journal of Zoology,* 1974, *52,* 889–906.

Tembrock, G. Land mammals. In T. A. Sebeok (Ed.), *Animal communication: Techniques of study and results of research.* Bloomington: Indiana University Press, 1968.

Thiessen, D. D. The roots of territorial marking in the Mongolian gerbil: A problem of species-common topography. *Behavior Research Methods and Instrumentation,* 1968, *1,* 70–76.

Thiessen, D. D. Footholds for survival. *American Scientist,* 1973, *61,* 346–351.

Thiessen, D. D., Clancy, A. N., & Goodwin, M. Harderian pheromone in the Mongolian gerbil, *Meriones unguiculatus. Journal of Chemical Ecology,* in press.

Thiessen, D. D., Friend, H. C., & Lindzey, G. Androgen control of territorial marking in the Mongolian gerbil. *Science,* 1968, *160,* 432–434.

Thiessen, D. D., Lindzey, G., & Nyby, J. The effects of olfactory deprivation and hormones on territorial marking in the male Mongolian gerbil (*Meriones unguiculatus*). *Hormones and Behavior,* 1970, *1,* 315–325.

Thiessen, D. D., Owen, K., & Lindzey, G. Mechanisms of territorial marking in the male and female Mongolian gerbil (*Meriones unguiculatus*). *Journal of Comparative and Physiological Psychology,* 1971, *77,* 38–47.

Thiessen, D. D., Regnier, F. E., Rice, M., Goodwin, M., Isaacks, N., & Lawson, N. Identification of a ventral scent marking pheromone in the male Mongolian gerbil (*Meriones unguiculatus*). *Science,* 1974, *184,* 83–85.

Thiessen, D. D., Wallace, P., & Yahr, P. Comparative studies of glandular scent marking in an Israeli gerbil (*Meriones tristrami*). *Hormones and Behavior,* 1973, *4,* 143–147.

Thiessen, D. D., & Yahr, P. Central control of territorial marking in the Mongolian gerbil. *Physiology and Behavior,* 1970, *5,* 275–278.

Thiessen, D. D., Yahr, P., & Owen, K. Regulatory mechanisms of territorial marking in the Mongolian gerbil. *Journal of Comparative and Physiological Psychology,* 1973, *32,* 382–383.

Tiefer, L. Gonadal hormones and mating behavior in the adult golden hamster. *Hormones and Behavior,* 1970, *1,* 189–202.

Vandenbergh, J. G. Effects of gonadal hormones on the flank gland of the golden hamster. *Hormone Research,* 1973, *4,* 28–33.

Vosseler, F. Beitrage zur Kenntnis der Fossa (*Cryptoprocta ferox Benn*) und ihrer Fortpflanzung. *Zoologische Garten NF.,* 1929, *2,* 1–9.

Wales, N. A. M., & Ebling, F. J. The control of the apocrine glands of the rabbit by steroid hormones. *Journal of Endocrinology,* 1971, *51,* 763–770.

Wallace, P., Owen, K., & Thiessen, D. D. The control and function of maternal scent marking in the Mongolian gerbil. *Physiology and Behavior,* 1973, *10,* 463–466.

Werner, H. J., Dalquest, W. W., & Roberts, J. H. Histology of the scent gland of the Peccaries. *Anatomical Record,* 1952, *113,* 71.

Whitehead, G. K. *Deer of the world.* New York: Viking Press, 1972.

Whitsett, J. M. The development of aggressive and marking behavior in intact and castrated male hamsters. *Hormones and Behavior,* 1975, *6,* 47–57.

Wilson, E. O. Chemical systems. In T. A. Sebeok (Ed.), *Animal communication.* Bloomington: Indiana University Press, 1968.

Wilson, E. O., & Bossert, W. H. Chemical communication among animals. *Recent Progress,* 1963, *19,* 673–716.

Yahr, R., & Thiessen, D. D. Steroid regulation of territorial scent marking in the Mongolian gerbil (*Meriones unguiculatus*). *Hormones and Behavior,* 1972, *3,* 359–368.

Young, J. *The life of vertebrates.* Oxford: Clarendon Press, 1950.

Zannier, R. Verhaltensuntersuchungen an der Zwergmanguste Helogale undulatarufula im Zoologischen Garten Frankfurt am Main. *Zeitschrift für Tierpsychologie,* 1965, *22,* 672–695.

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