

22. M. M. Ludlow, *Planta* **91**, 285 (1970).
23. G. E. Hutchinson, in *The Earth as a Planet*, G. P. Kuiper, Ed. (Univ. of Chicago Press, Chicago, 1954), pp. 371-433.
24. H. D. Holland, in *Origin and Distribution of the Elements*, L. H. Ahrens, Ed. (Pergamon, Oxford, 1968), pp. 949-954.
25. A. G. Fischer [*Proc. Nat. Acad. Sci. U.S.* **53**, 1205 (1965)] advocates the existence of cryptogams in soil before the Silurian.
26. E. I. Rabinowitch, *Photosynthesis and Related Processes* (Interscience, New York, 1945-1956), vols. 1-3; R. H. Whitaker, *Communities and Ecosystems* (Macmillan, New York, 1970).
27. B. Mason, *Principles of Geochemistry* (Wiley, New York, ed. 3, 1966).
28. H. Suess, *Proc. Nat. Acad. Sci. U.S.* **53**, 1225 (1965).
29. W. S. Broecker, *J. Geophys. Res.* **75**, 3553 (1970).
30. A. M. Macgregor, *S. African J. Sci.* **24**, 155 (1927).
31. W. W. Rubey, in *Crust of the Earth*, A. Poldervaart, Ed. (Geological Society of America, New York, 1955), pp. 631-650.
32. P. E. Cloud, Jr., *Science* **148**, 27 (1965).
33. Among other curious conclusions, M. G. Rutten [*Space Life Sci.* **2**, 5 (1970)] maintains that there was a regulation of oxygen concentration at the Pasteur point, because with a greater concentration respiration would increase and use the oxygen, whereas with a lower concentration fermentation would increase and oxygen would accumulate. However, both respiration and fermentation are oxidative processes (see arguments elsewhere in this article for additional points).
34. M. K. Hubbert, in *Resources and Man*, Committee on Resources and Man of the National Academy of Sciences, Eds. (Freeman, San Francisco, 1969), pp. 157-242.
35. A. B. Ronov [*Geokhimiya* **8**, 175 (1964); translated in *Geochem. Int.* (1964), p. 713] believes there was an immense outgassing about 2.6×10^9 years ago in conjunction with the emplacement of half or more of the earth's plutons, but if this event is real it may be related to the closest approach of the moon [J. A. Cooper, J. R. Richards, F. D. Stacey, *Nature* **215**, 1256 (1957)], which would undoubtedly affect the atmosphere also. The "anorthosite event" and other later phenomena [N. Herz, *Science* **164**, 944 (1969); P. E. Cloud, Jr., *ibid.* **160**, 729 (1968)] have also been related to the moon's approach.
36. It is not impossible that world photosynthesis was then much more than it is today. I will present elsewhere a mechanism for controlling the ratio of nitrogen to phosphorus in the ocean; the mechanism implies that nitrogen is not, and that phosphorus may be, the major limiting factor for total marine photosynthesis. The mechanism requires the presence of nitrogen-fixing blue-green algae. The similarity of *Gunflintia* to the nitrogen-fixer *Anabaena* in morphology, as suggested by G. E. Hutchinson (personal communication), makes plausible a physiological similarity. If more phosphorus was present than there is now, and Hutchinson suggests this might have been the case because of the prevalence of ferrous rather than ferric iron, then the rate of photosynthesis may also have been larger.
37. C. F. Davidson, *Proc. Nat. Acad. Sci. U.S.* **53**, 1194 (1965).
38. I am an ecologist, not a geochemist, and the viewpoint of this article comes readily from familiarity with the formally similar problem of regulation of population density of organisms. In fact, the question as to the cause of regulation of oxygen seemed so obvious that I assumed the answer was well known until I asked what it was. Several areas of science relate to the subject of this article, and I am grateful to the following people for information, comments, or reading of the manuscript: R. G. Alderfer, A. T. Anderson, Jr., W. S. Broecker, S. Chandrasekhar, R. N. Clayton, P. E. Cloud, Jr., H. D. Holland, J. D. Hudson, G. E. Hutchinson, D. A. Janzen, J. P. Lodge, B. Mason, P. Meyer, E. K. Peterson, T. J. M. Schopf, J. M. Witting, and A. M. Ziegler. Partly supported by a research career development award from PHS.

Mammalian Scent Marking

Mammals mark when dominant to and intolerant of others, not just when they possess a territory.

Katherine Ralls

Most mammals have a highly developed olfactory sense which they employ in social communication, using chemical signals originating in urine, feces, or cutaneous scent glands (1). Many use specialized motor patterns to deposit the chemical signals on environmental objects or other animals of the same species; such behavior is referred to as scent marking or marking (2). Very little is known about the chemical nature of these signals although the composition of some scent gland secretions has been studied by perfume chemists (3). One of the major components of the secretion of the tarsal gland of male black-tailed deer, *Odocoileus hemionus columbianus*, has recently been identified (4).

Although marking has long been recognized as an important form of communication in mammals, our understanding of the messages communicated

by the marks has remained vague due to lack of information on the stimulus situations which elicit marking and the reactions of other animals to the marks.

Several general kinds of marking can be distinguished on the basis of the functions which the marks seem to serve. For example, marks or scents may be used primarily for laying trails, as in the slow loris, *Nycticebus coucang* (5); for alarm signals, as in mice (6) and probably rats (7); for individual recognition, as in mice and deer (8); for group recognition, as in the sugar glider, *Petaurus breviceps* (9); for species or subspecies recognition, as in voles and mice (10); for sexual attraction, as in many estrous female mammals (11); and as primer pheromones influencing reproductive processes, as in mice (12). One secretion may serve a number of these functions (9).

A very common kind of marking is

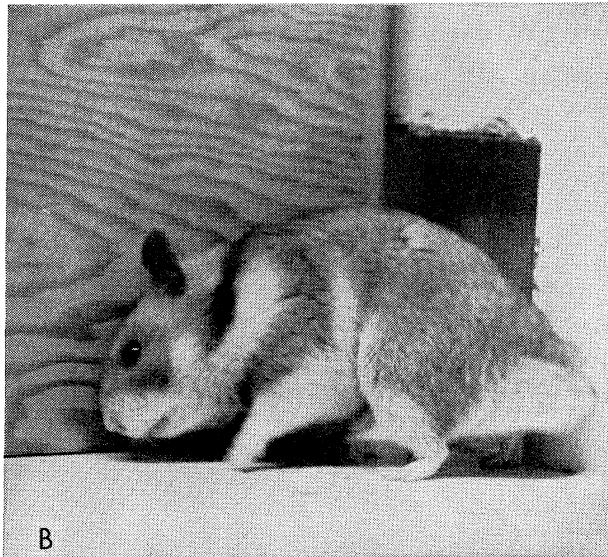
that which, since the classic paper by Hediger in 1949 (13), has been characterized as "territorial marking." This terminology implies that the marks serve to identify a territory, that is, a fixed area of land which the marking individual will defend against rivals of the same species. Such an interpretation is no doubt correct for some species, but it should not be assumed that all marking is territorial.

Among Hediger's examples of "territorial marking" were the ritualized urination and defecation of the black rhinoceros, *Diceros bicornis* (14), and the marking with the retrocornal gland shown by the chamois, *Rupicapra rupicapra* (13). Recently, both of these species have been studied in the field. Schenkel (15, 16) reports that the black rhinoceros is not territorial; Krämer (17) finds that the marking of the chamois is not associated with the possession of a territory. In both cases, it must be some factor other than the possession of a territory which stimulates the animals to mark. Several experimental studies of this kind of scent marking carried out within the last 5 years (9, 18-32), have provided a closer look at the stimulus situations which elicit marking. The species which have been studied experimentally tend to mark frequently in any situation where

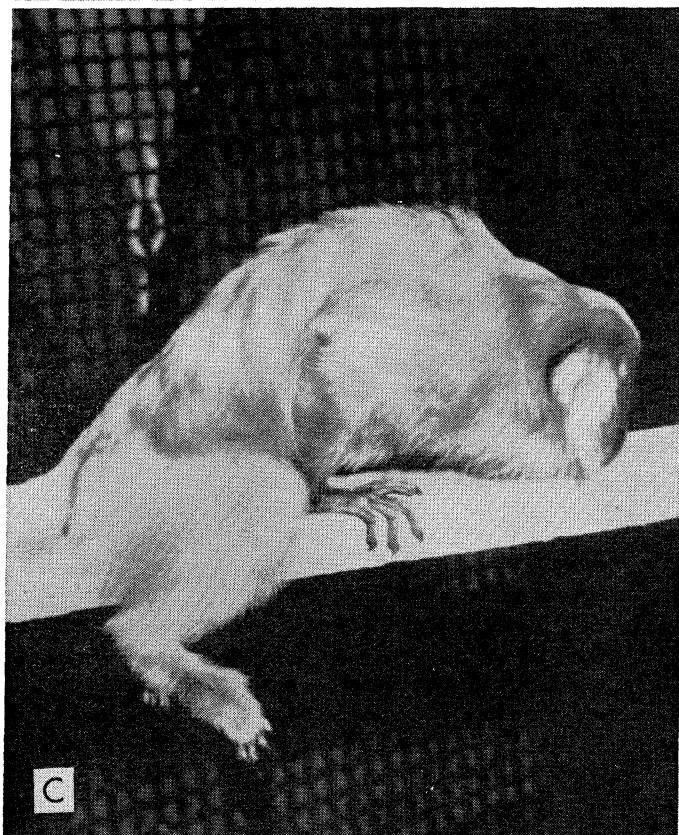
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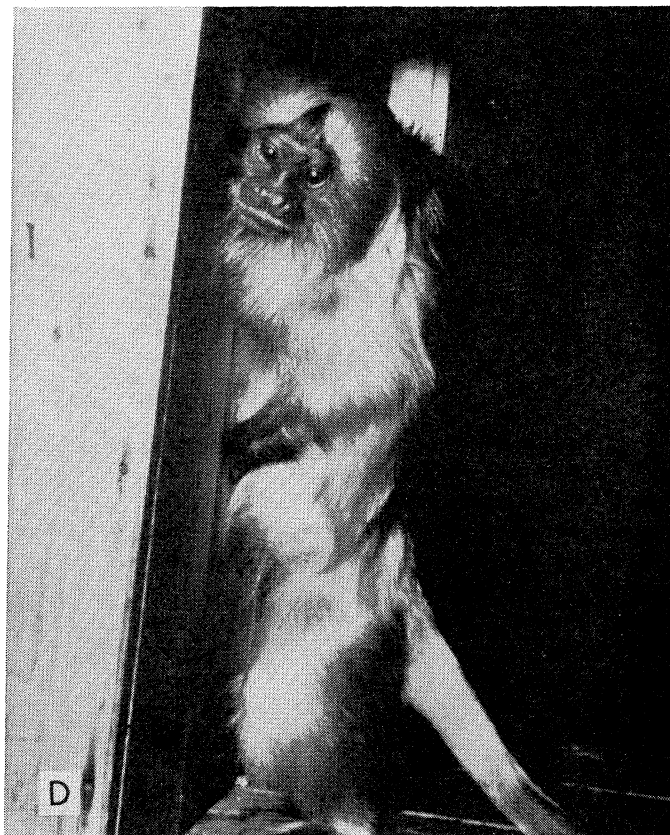
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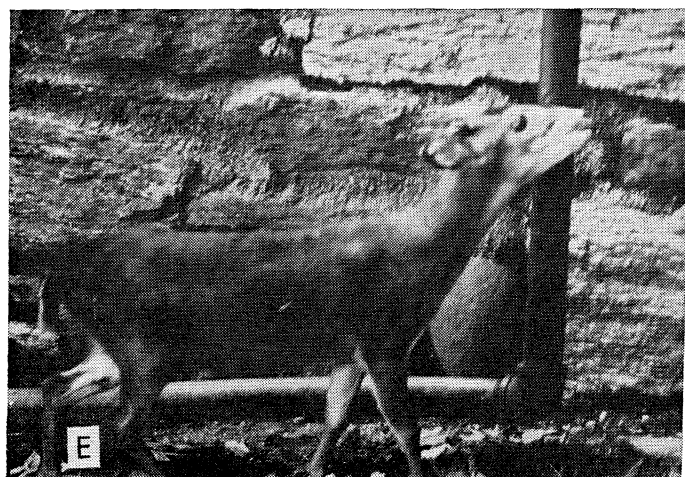
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D



E



F

Table 1. Number of marks with chin gland in 1 hour by rabbits of known social status. Dominant rabbits mark more than do subordinate ones. Each enclosure contained five adult rabbits [after (19, 20)].

Status	Number of marks with chin gland in 1 hour	
	Enclosure 1	Enclosure 2
	<i>Males</i>	
Dominant	8	6
Subordinate	0	1
	<i>Females</i>	
Dominant	6	2
Subordinate	3	1
Third-rank	0	0

they are both intolerant of and dominant to other members of the same species. In other words, they mark when they are likely to attack another member of the same species, and are likely to win if they do attack. Such behavior will occur in territorial defense but is by no means restricted to territorial situations.

Association of Marking and Dominance

There is a striking correlation between a high rate of marking and high social status or dominance. The dominance is expressed in various ways, depending upon the prevailing social system. An animal which marks frequently may be the dominant individual in a group, the dominant individual in a fixed area or territory, both of these, the dominant individual only when close to certain other animals (for example, a male near females) (33), or a solitary individual which does not defend a territory but which habitually wins agonistic encounters with other animals of the same species. The degree of crowding may affect the type of dominance system within a species. In captive groups of mice, a shift from territorial dominance at low densities

Fig. 1. Scent glands and marking methods of various mammals. (A) Male (top) and female (bottom) sugar glider. The frontal gland is on the forehead of the male [T. Schultze-Westrum]. (B) Golden hamster marking with flank gland [R. Johnston]. (C) Female golden lion marmoset marking with circumgenital glands [G. Eppl]. (D) Female golden lion marmoset marking with sternal gland [G. Eppl]. (E) Male Maxwell's duiker marking with maxillary gland [K. Ralls]. (F) Male (right) and type female A (left front) Maxwell's duiker pressing their maxillary glands together. Type B female (left rear) does not participate [K. Ralls].

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to individual dominance at high densities has been demonstrated (34).

One of the first reports to link a high rate of marking with dominance was Schultze-Westrum's study of the sugar glider (9, 18). The sugar glider or flying phalanger (Fig. 1A), a small marsupial, lives in social nesting communities consisting of up to six adults and their young. Each community has a territory. Male sugar gliders produce odors in the frontal gland, the sternal gland, and the cloacal region. They use the frontal gland to mark other members of the community. They actively mark their territory in several ways—by rubbing their sternal, anal, and flank regions on objects, and by stereotyped chewing and foot-rubbing movements. Female sugar gliders do not possess the specialized glands of the male. They rarely mark. The important point is that the one or two dominant males in each community perform almost all of the marking, both of community members and of the territory.

The highest rates of marking are also found in dominant rabbits as studied by Mykytowycz (19-21). Rabbits live in small social groups, each group occupying a territory. There is a hierarchy among the males of a territory and a separate hierarchy among the females. A dominant pair of rabbits rules each territory.

Rabbits have two scent glands which are associated with social dominance and territoriality. They deposit the secretion of one, the submandibular or chin gland, by a form of marking called chinning. Dominant males chin more frequently than do subordinate males and dominant females chin more frequently than do subordinate females (Table 1).

Rabbits deposit the secretion of the other, the anal gland, with their feces. It is difficult to determine the frequency of anal marking because not all the feces of an individual carry the anal gland secretion. It seems, nevertheless, that dominant animals do deposit either a larger amount of anal gland secretion or a more potent secretion. Rabbits scatter the unmarked feces about, and pile up the marked feces at prominent locations in their territory. The feces of dominant male and female rabbits which are marked with the secretion smell more strongly to humans than do the unmarked feces, although in subordinate males no differences in odor between the kinds of feces are detectable (22).

Table 2. Mean weight of bodies, central chin glands, and anal glands of rabbits of known social status. Dominant rabbits have larger glands than do subordinate ones [after (19, 20)].

Status	Rabbits (No.)	Mean weight of body (g)	Mean weight of central chin gland (mg)	Mean weight of anal gland (mg)
		<i>Male</i>		
Dominant	6	1316	320	
Subordinate	4	1231	152	
Dominant	6	1292		2158
Subordinate	6	1217		594
		<i>Female</i>		
Dominant	6	1250		1515
Subordinate	6	1146		434

Mykytowycz has also shown that both the chin and anal glands are larger in dominant males than in subordinate males (Table 2). Dominant males tend to be older and heavier than subordinate males, but the size of their glands is much greater than would be predicted simply on the basis of their additional body weight.

The relation between marking rate and social status in the golden hamster has been studied by Johnston (23). Although little is known of the social life of the golden hamster in its natural environment, it is clear from their behavior in captivity that hamsters are not gregarious animals. It is probable that adults live solitarily and that the only social group consists of a female and her litter. Hamsters mark with a gland on their flank (Fig. 1B).

Johnston allowed pairs of male hamsters, one pair at a time, into a neutral area. He called the winner of the resulting fight the dominant male and the loser the subordinate male. After the fight, each male was placed in the empty home cage of his opponent and the number of times he marked was recorded. In every case, the dominant male marked much more frequently than did the subordinate male (Table 3).

The relation between marking rate and social status in the Mongolian gerbil has been investigated by Thiessen and his colleagues (24-26). Although the behavior of wild Mongolian gerbils is unknown, captive gerbils mark objects in their environment with the secretion from a mid-ventral gland. Males mark at least twice as frequently as do females.

The experimental procedure used by Thiessen (25) is the inverse of that used by Johnston with hamsters. Thiessen

recorded the marking frequencies of male gerbils under standard conditions. He then assigned the animals to pairs on a random basis and allowed them to encounter each other. As expected, the males that had high initial rates of marking tended to be dominant.

Epple (27-29) has found that dominant common marmosets, *Callithrix jacchus*, of both sexes mark more frequently than subordinate animals do. Little is known about the social organization of wild marmosets. In captive groups, one adult male dominates all other adult males but tolerates females and juveniles, and one adult female dominates all other adult females but tolerates males and juveniles. The dominant male and the dominant female do not compete with each other. No rank order occurs among the subordinate individuals. Only the dominant female reproduces.

Epple observed three groups (28), each consisting of a dominant male, a dominant female, and a varying number of subordinate and juvenile animals.

Captive marmosets mark frequently with their circumgenital glands (Fig. 1C). Dominant males usually mark more than subordinate and juvenile males do, and dominant females mark more than subordinate females (Table 4).

Some individuals also mark with a gland on their ventral surface called a sternal gland (Fig. 1D) (29). This gland is best developed in the highest-ranking individuals of each sex. However, only high-ranking males mark with the

Table 3. Mean number of marks with flank gland by male golden hamsters after encounters with other males. Each animal was placed in his opponent's cage and the number of marks was recorded (12 10-minute tests). The dominant male, who won the fight resulting from the encounter, marked more than did the subordinate one every time [after (23)].

Pair	Mean number of marks with flank gland by	
	Dominant male	Subordinate male
B-22	20.6	5.2
B-21	23.6	0.02
15-17	26.6	2.1
25-10	17.4	1.2
26-12	13.2	1.25
11-23	15.7	0.5

sternal gland and even they mark in this way very infrequently. In other species of marmoset, both males and females mark frequently with the sternal gland.

In my study of Maxwell's duiker (31, 32), I found correlation between marking frequency and social status. Maxwell's duiker is a small antelope, 13 inches (32 centimeters) at the shoulder, that lives in the forests of West Africa. Almost nothing is known about the life of duikers in the wild. Judging from my observation of captive animals, I think they probably live in pairs on territories.

Like many antelopes, duikers have a large gland underneath each eye. Both males and females frequently rub the secretion of this gland on objects in their environment (Fig. 1E). They also rub their glands on each other's glands.

A male and female, facing each other, press together the glands first on one side of their faces, and then on the other (Fig. 1F).

I divided nine duikers, at the Bronx Zoological Park, into three groups, each consisting of a male and two females. One of the two females in each group both marked with the male and groomed him much more frequently than the other female did. I call these females the type A female and the type B female, respectively.

Among the nine duikers the males marked objects in the environment most frequently (Table 5). The type A females marked about half as frequently as the males did, while type B females rarely marked. The type A female has a closer relationship with the male than the type B female does. She is not necessarily dominant over the type B female. The two types of females have not been observed to engage in any activities which would enable one to discern dominance.

The male duikers all marked with about the same frequency when they were in small, indoor cages (Table 5). However, each marked with a different frequency when his group was placed in a large enclosure (46 by 108 meters) containing dense shrubbery. Under these conditions, the dominant male marked most frequently and the lowest ranking male marked least frequently. It was easy to decide the dominance order of the males by observing the outcome of the fights which resulted when two males were placed together.

Pagès (35) has recently found that dominant pangolins mark more than subordinate ones do. Chamois mark more frequently when with a social partner than when alone; in pairs where the rank of both partners was known the dominant individuals marked a total of 82 times, whereas subordinates marked only 35 times (17). The association of high rates of marking with dominance, expressed in various ways in different social systems, thus may be a very widespread phenomenon in mammals.

Association of Marking with Intolerance of Conspecifics

Many species mark more frequently than usual after encounters with individuals with which they do not normally associate. The scents of these animals may have a similar effect. This

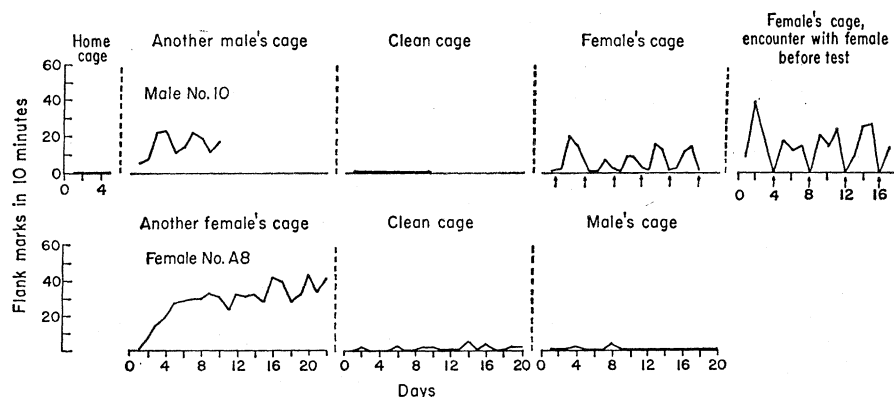


Fig. 2. (Top) Amount of flank marking by a male golden hamster under different test conditions. Males do little marking in their home cages or in clean cages. They mark more when placed in an empty cage belonging to either a male or female hamster. Cyclic variation of marking in cages that belong to females is correlated with the estrous cycle of the female—males do the least marking on the day the female is in estrus and the day after (23). (Bottom) Amount of flank marking by a female golden hamster under different test conditions. Females mark more in an empty cage belonging to another female than they do in one belonging to a male or a clean cage (23).

does not occur when they encounter individuals belonging to their own social group or their scents. The frequency of marking varies according to the sex of the strange individual: many species mark more frequently after encounters with members of their own sex than they do after encounters with members of the opposite sex.

A dominant male sugar glider marks frequently after smelling filter paper bearing scents from a male belonging to another social group; scents from the sternal, frontal, and anal regions of the strange male are equally effective (9). He does not mark more than usual after smelling filter paper bearing no scent or scent from a male belonging to his own social group, or scent from his own body. A male does not mark in response to scent from a female.

Rabbits mark with their chin glands and produce fecal pellets marked with anal gland secretion when a strange rabbit or a cloth impregnated with the smell of a strange rabbit is put into their cage (22). It has not been reported whether rabbits mark more frequently in response to a stranger of the same sex than to one of the opposite sex.

A male hamster marks frequently when placed in an empty cage belonging to another hamster of either sex; he marks infrequently in his own cage or in a clean cage (Fig. 2) (23). The amount of marking the male does in cages belonging to a female varies according to the day of her estrous cycle. He marks very little the day the female is in estrus and the day after estrus. The reduction in marking frequency shown by a male in the cage of an estrous female may be caused by her special vaginal secretion; in other experiments the addition of this secretion was sufficient to reduce male flank marking. A female hamster marks much more when placed in an empty cage belonging to another female than in that of a male (Fig. 2). Some females mark hardly at all in the cage of a male; some females do, but these will do so more frequently in cages of females than in cages of males.

A dominant male marmoset increases his marking frequency dramatically after a strange male has been present in his group. The frequency fails to increase or increases to a lesser degree after a strange female has been present (28). Juvenile males also increase their marking after meeting a strange male (Table 4). A dominant female marmoset increases her marking frequency

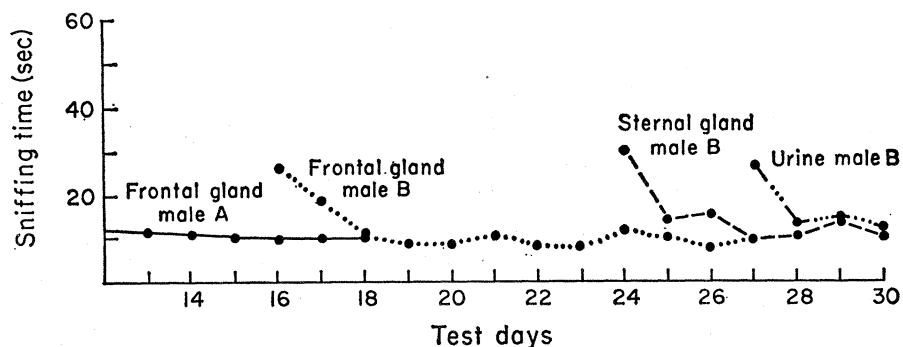


Fig. 3. Evidence that male sugar gliders can distinguish the scents from the same body regions of two different males and from the different body regions of an individual male. Average time spent sniffing at various scents by two dominant male sugar gliders (sec/5 min. test). Filter paper bearing the scent of the frontal gland of male A was presented daily for 15 days until the males had habituated to the scent and spent a low and relatively constant amount of time sniffing it. On day 16, filter paper bearing the scent of the frontal gland of male B was also presented and was sniffed for a much greater time than the scent of male A's frontal gland, demonstrating that the test males could distinguish the two scents. The same method was used to show that the test males could distinguish the frontal gland scent of male B from the sternal scent of male B and the latter from the urine scent of male B [after (17)].

much more after a strange female has been present than after a strange male has been in the cage (Table 4). Similarly, a male duiker marks more frequently after another male has been temporarily present in his group but shows no increase after an extra female has been present (Table 5) (32). One of the type A females, female 1, marked more frequently after an extra female had been present but did not do so after an extra male had been present (Table 5). The second type A female, female 2, behaved in the same way. However, the third type A female, female 3 did not. At the time of the experiment, her physical condition was declining, and soon afterwards she lost her type A position to the other female of her group. A

type B female does not mark more frequently after either an extra male or an extra female has been present. A type B female does mark more frequently, however, when her group is placed in a large outside enclosure, and she is able to escape from proximity of other duikers.

The Motivation of Marking

Several methods are available for inferring the motivation of a given act such as marking. These methods are, in order of increasing strength: (i) fine morphological analysis, whereby one shows that the given act, a fragment of a display, is identical to a fragment of another display with a known

Table 4. Mean number of marks per hour with the circumgenital glands by marmosets of known social status. Dominant animals tend to mark more than do subordinate ones. Dominant animals increase their marking more after a stranger of the same sex has been present in the group than they do after a stranger of the opposite sex has been present [after (28)].

Status and age	Group membership	Mean number of marks per hour with the circumgenital glands		
		Without strangers	With strange male	With strange female
<i>Males</i>				
Dominant adult	I	4.61	52.00	2.50
Dominant adult	II	16.58	54.87	11.50
Dominant adult	III	9.09	43.28	21.70
Subordinate juvenile	I	5.07	10.50	1.25
Subordinate juvenile	II	5.17	11.34	2.16
Subordinate adult	II	3.40	1.00	2.20
<i>Females</i>				
Dominant adult	I	13.92	12.00	20.50
Dominant adult	II	9.70	18.37	36.83
Dominant adult	III	13.27	13.85	36.50
Subordinate juvenile	I	1.69	0.66	1.00
Subordinate adult	III	1.84	7.16	1.50
Subordinate adult	I	5.45	8.42	12.50

motivation; (ii) correlation of the act with stimulus situations which cause a known motivational state; and (iii) close temporal association of the act with acts which result from a known motivational state. The first method is not of much help with regard to marking, but the other two methods have yielded a great deal of pertinent evidence. Frequent, vigorous, "high-intensity" marking occurs at times when there is reason to infer that the animal is motivated to aggression.

The strength of the correlation between marking and motivation to aggression declines with the vigor and frequency of the marking. Little can be said about the motivation of less vigorous marking—it may be entirely different. Ewer (2) considers that animals mark both to reassure themselves and to threaten other individuals, with the relative importance of the two factors varying from case to case. In the animals which have been studied experimentally so far (9, 18–32), the threatening, aggressive component seems to predominate although male sugar gliders are more likely to attack if their own scent is present (36).

First, let us review the evidence that marking occurs in stimulus situations which are known or believed to give rise to aggressive motivation. One such situation is the possession of a territory. It is well known that a territory holder within his territory is more likely to initiate an attack than an animal which does not have a territory. The same is true of the dominant animal in a group with a social hierarchy. It is more likely to exhibit aggression than is a subordinate animal. A stimulus which is especially effective in eliciting aggression from a territory holder or a dominant animal is the appearance of a strange conspecific of the same sex: as we saw earlier, such intruders, or their scents, are also extremely effective in eliciting marking. In some cases even the isolated scent of a strange member of the species suffices to elicit aggression toward conspecifics. Dominant male sugar gliders encountering the scent of a foreign male in their cage react not only by marking but also by increased aggression toward males in neighboring cages from which they are separated by wire partitions (9). The male brushtail possum *Trichosurus vulpecula* performs a threat display in response to the anal gland secretion of another male, but not in response to the anal gland secretion of a female (37). The urine of male mice is believed to pos-

Table 5. Mean number of marks with maxillary gland by Maxwell's duikers on objects in their environment (per 10 minutes). Males mark more than do females. Type A females mark more than do type B females. Males and type A females tend to increase their marking activity more after a conspecific of the same sex has been present than they do after one of the opposite sex has been present (32).

Group membership	Marking activity when with own group	Marking activity after presence of additional	
		Male	Female
<i>Males</i>			
I	6.6	15.2	6.1
II	5.8	10.7	6.2
III	4.4	8.6	4.1
<i>Type A females</i>			
I	3.5	3.7	18.6
II	3.4	3.1	12.2
III	1.5	0	1.7
<i>Type B females</i>			
I	0.06	0	0.09
II	0	0.1	0
III	0.04	0	0.03

sess a pheromone which increases aggression in other male mice (38).

Among internal stimuli, androgens increase the readiness of many species to engage in aggressive acts (39). It is also known that androgens influence many of the glands used for marking. The chin and anal glands of the rabbit (19, 20), the flank glands of the golden hamster (40), and the ventral gland of the gerbil (26) have all been shown to be androgen dependent. Although an increase in the amount of marking with increasing dosage of androgen has only been shown in gerbils, in most species individuals with large glands probably mark more than do those with small ones. This is well documented in rabbits (19).

Let us now examine the evidence for the temporal correlation of marking with acts thought to be caused by motivation to aggression. When two male duikers mark each other, it is always the prelude to a fight, and I never observed fighting without this introductory marking. When duikers mark environmental objects at a high frequency, they perform other behavior patterns that are suggestive of motivation to aggression—they thrash the marked object with their horns, and paw vigorously at the ground with their front legs (32). Similar behavior has been observed in many other species. The roe deer, *Capreolus capreolus*, marks branches at territorial boundaries with the secretion from a forehead gland, thrashes the branches with its antlers, and scrapes up the surrounding ground with its forelegs (41). The combination of urine mark-

ing, thrashing of shrubs with the antlers, and digging or pawing with the forefeet as a threat display has been described in reindeer *Rangifer tarandus* (33), Roosevelt elk *Cervus canadensis roosevelti*, and black-tailed deer *Odocoileus hemionus columbianus* (42). Male black-tailed deer also urinate on their tarsal tufts and rub them together when threatening each other (43).

The ritualized urine marking ceremony of the black rhinoceros involves similar components: urinating on a plant, smashing it with the nasal horn, and scraping the earth around it with kicks of the hind legs. Schenkel (16) describes this display as having a "showing off" character, with elements of symbolized aggression addressed to the plant as a substitute for a rival (44).

Male *Lemur catta* engage in "stink-fights," which Jolly (45) describes as follows: "A stink-fight is a long series of palmar-marking, tail-marking, and tail-waving directed by two males toward each other. . . . First one marks, then the other, with pauses in between . . . the more aggressive male gradually moves forward, the other retreats . . . the more aggressive one palmar-marks branches the other has marked. A stink-fight may go on from 10 minutes to an hour."

Male coatis, *Nasua nasua*, often mark with urine when they threaten each other (46). The Uinta ground squirrel, *Citellus armatus*, protrudes the papilla of its anal scent gland only during threat behavior (47). In the chamois, marking and broadside threats occur in close temporal proximity, whereas marking and submissive behavior never occur together (17). In marmosets, marking is often associated with an aggressive threat display, "genital presenting," and actual attacks (28). The posture of a marking hamster indicates that it is prepared to attack (23).

Effects of Marking

It has often been suggested that marking may enable an animal to attain and maintain dominance or the possession of a territory, but experimental evidence on this point is sparse. In some cases, marking may help an animal to attain or maintain dominance by serving as a threat. Epple (28) believes that the circumgenital and sternal markings of marmosets act in this way. In other cases, marking by one individual may keep the other individuals of the group in an underdeveloped physiologi-

cal condition by distributing primer pheromones. Marking by a dominant male sugar glider, according to Schultze-Westrum (9, 18) has such an effect on other males in the community. If the dominant male is removed from a group the marking frequencies of subordinate males increase. Even if a dominant animal is marking frequently, the marking is not necessarily the means by which it is maintaining its status. The aggressiveness of dominant animals would tend to keep them in a dominant position regardless of whether or not they marked (48). The frequent copulations of dominant males may also play a role. Copulation leads to significant increases in plasma testosterone in male rabbits (49), which in turn would tend to maintain their dominance.

Marking with More Than One

Source of Scent

Many species mark with more than one source of scent in response to one stimulus or set of stimuli. For example, in response to the scent of a strange male, a male sugar glider marks in several different ways by rubbing with his feet, his flanks, and by chewing. He marks in all these ways in response to scent taken from any part of the stranger's body; the relative proportions of the three ways of marking remain constant regardless of the stimulus. One might conclude that a male marks in this way because he is unable to distinguish between the scents from different parts of the body of another male. This conclusion is not correct. A male sniffs only briefly at the scent from a given part of another male's body after it has been repeatedly presented to him but sniffs for a longer period when a scent from a different part of the same male's body is presented (Fig. 3) (9).

A rabbit marks with both chin and anal glands when it smells a strange rabbit. According to Mykytowycz (21), a rabbit uses both glands, as well as urine, to mark its territory. Male gerbils sometimes mark with a chin gland in addition to the ventral gland (30), but we have no details. A dominant male marmoset marks with the sternal gland in the same situations in which he marks with his circumgenital glands, in particular when another male or his scent has been present. Urine also may serve as a source of scent in marmosets (28).

When an animal marks with more

than one source of scent in response to one stimulus, is it sending several messages or is it sending the same message (or set of messages) in different ways? At present we cannot answer this question. If only a single message is conveyed, why should an animal send the same message with two different signals? Perhaps such a method of transmission would, under some conditions, increase the probability of the message being received. Each signal might be effective under a different set of environmental conditions. For example, one scent might be more likely to survive under humid conditions, whereas the other might be more likely to survive under dry conditions. It is equally possible that the messages are different but that we are at present unable to discern the differences.

Summary

Mammals mark frequently in any situation where they are both intolerant of and dominant to other members of the same species. In other words, they mark when they are likely to attack another member of the same species, and are likely to win if they do attack. Such a situation occurs, as Hediger (13) pointed out, in connection with territoriality but it also occurs in other kinds of social systems. Frequent, vigorous marking occurs at times when there is reason to infer that the animal is motivated to aggression. The effects of marks and marking upon other individuals are poorly understood. Many species mark with more than one source of scent in response to one stimulus or set of stimuli.

References and Notes

1. J. Schaffer, *Die Hautdrüsenorgane der Säugtiere* (Urban and Schwarzenberg, Berlin, 1940); M. Gabe, in *Traité de Zoologie*, P. P. Grasse, Ed. (Masson, Paris, 1967), vol. 16.
2. R. F. Ewer, *Ethology of Mammals* (Plenum, New York, 1968), pp. 104-133.
3. E. Lederer, *Progr. Chem. Org. Nat. Products* 6, 87 (1950); B. Kingston, *Proc. 2nd Int. Congr. Endocrinol. (London)*, part 1, p. 209.
4. R. Brownlee, R. Silverstein, D. Müller-Schwarze, A. Singer, *Nature* 221, 284 (1969); D. Müller-Schwarze, *ibid.* 223, 526 (1969).
5. E. Seitz, *Z. Tierpsychol.* 26, 73 (1969).
6. H. Müller-Velten, *Z. Vergl. Physiol.* 52, 401 (1966).
7. J. Valenta and M. Rigby, *Science* 161, 599 (1968).
8. J. Bowers and B. Alexander, *ibid.* 158, 1208 (1967); D. Müller-Schwarze, *Amer. Zool.* 7, 430 (1967).
9. T. Schultze-Westrum, *Z. Vergl. Physiol.* 50, 151 (1965).
10. J. Godfrey, *Proc. Roy. Phys. Soc. Edinburgh* 27, 47 (1958); K. Rauschert, *Biol. Zentralbl.* 82, 653 (1963); R. Moore, *Amer. Midl. Natur.* 73, 85 (1965).
11. R. P. Michael and E. B. Keverne, *Nature* 218, 746 (1968); D. Pfaff and C. Pfaffmann, in *Olfaction and Taste*, C. Pfaffmann, Ed. (Rockefeller Univ. Press, New York, 1970).
12. W. K. Whitten, *Advan. Reprod. Physiol.* 1, 155 (1966); F. H. Bronson, in *Reproduction and Sexual Behavior*, M. Diamond, Ed. (Indiana Univ. Press, Bloomington, 1968).
13. H. Hediger, *Bijdr. Tot Dierkunde* 28, 172 (1949).
14. ———, *Explorations des parcs nationaux du Congo Belge* (Institut des Parcs Nationaux du Congo Belge, Brussels, 1951).
15. R. Schenkel, *Z. Tierpsychol.* 23, 593 (1966).
16. ——— and L. Schenkel-Hulliger, *Ecology and Behaviour of the Black Rhinoceros* (Parey, Hamburg, 1969), pp. 96-97.
17. A. Krämer, *Z. Tierpsychol.* 26, 889 (1969).
18. T. Schultze-Westrum, in *Olfaction and Taste*, C. Pfaffmann, Ed. (Rockefeller Univ. Press, New York, 1970); T. Schultze-Westrum, in preparation.
19. R. Mykytowycz, *Anim. Behav.* 13, 400 (1965).
20. ———, *CSIRO Wildl. Res.* 11, 11 (1966).
21. ———, *Sci. Amer.* 218, 116 (1968).
22. E. Hesterman and R. Mykytowycz, *CSIRO Wildl. Res.* 13, 71 (1968).
23. R. Johnston, thesis, Rockefeller University (1970).
24. D. Thiessen, *Behav. Res. Methodol. Instr.* 1, 70 (1968); ———, S. Blum, G. Lindzey, *Anim. Behav.*, in press.
25. D. Thiessen, G. Lindzey, S. L. Blum, P. Wallace, in preparation.
26. D. Thiessen, H. Friend, G. Lindzey, *Science* 160, 432 (1968); A. Feldman and O. G. Mitchell, *J. Morphol.* 125, 3037 (1968).
27. G. Epple, *Folia Primatol.* 7, 37 (1967).
28. ———, *ibid.*, 13, 48 (1970).
29. ——— and R. Lorenz, *ibid.* 7, 98 (1967).
30. D. Thiessen and P. Yahr, *Amer. Zool.* 9, 1069 (1969).
31. K. Ralls, *ibid.*, p. 1071.
32. ———, in preparation.
33. Y. Espmark, *Anim. Behav.* 12, 159 (1964).
34. P. Crowcroft, *J. Mammal.* 36, (1955); D. Davis, *Brit. J. Anim. Behav.* 6, 207 (1958).
35. E. Pagès, *Biol. Gabon.* 4, 354 (1968).
36. T. Schultze-Westrum and B. Braun, in preparation.
37. J. Thomson and F. Pears, *Victoria Nat.* 78, 306 (1962).
38. R. Mugford, *Nature* 226, 967 (1970).
39. A. Guhl, in *Sex and Internal Secretions*, W. C. Young, Ed. (Williams & Wilkins, Baltimore, 1961).
40. F. La Velle, *Carnegie Inst. Publ. No. 592, Contrib. Embryol.* 34, 19 (1951).
41. R. Prior, *The Roe Deer of Cranborne Chase* (Oxford Univ. Press, London, 1968), pp. 69-71.
42. W. Graf, *J. Mammal.* 37, 165 (1965); T. Struhsaker [Z. *Tierpsychol.* 24, 80 (1967)] suggests that the fluid emitted by elk may be ejaculate rather than urine. It is interesting to note the use of this pattern of marking, thrashing, and pawing within the cervids regardless of the social system of each species. It is used by species with primarily solitary modes of existence such as the black-tailed deer, in species in which dominant males maintain a "mobile territory" around a group of females, such as the reindeer, and by a species which maintains a fixed territory, the roe deer.
43. R. Brownlee, R. Silverstein, D. Müller-Schwarze, A. Singer, *Nature* 221, 284 (1969).
44. D. Burckhardt, cited in (17), has suggested that marking in general may be thought of as a battle with a rival-substitute, with which the deposition of scent has become associated.
45. A. Jolly, *Lemur Behavior: a Madagascar Field Study* (Univ. of Chicago Press, Chicago, 1966).
46. J. Kaufmann, *Univ. Calif. Publ. Zool.* 60, 95 (1962).
47. D. Balph and A. Stokes, *Amer. Midl. Natur.* 69, 106 (1963).
48. In the case of the sugar glider, no agonistic behavior occurs within a community under normal conditions, so dominance cannot be maintained by aggression in this species.
49. G. Haltmeyer and K. Eik-nes, *J. Reprod. Fert.* 19, 273 (1969).
50. I thank C. Pfaffmann for generous support, P. Marler for criticism and support, R. Johnston for criticism and permission to include unpublished data, G. Epple and T. Schultze-Westrum for criticism and photographs, D. Griffin for criticism, and W. Conway and B. House for assistance at the zoo. Supported by NIH training grant GM 1789-02/03 to Dr. Pfaffmann and NSF grant GB 7143 to Dr. Marler.