

SOCIAL SCENTS IN HAND-REARED PRONGHORN (*ANTILOCAPRA AMERICANA*)

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ABSTRACT

Three male and one female pronghorn (*Antilocapra americana*) were taken in the wild when a few hours to three days old and were hand-raised. The development of their behaviour was studied with particular emphasis on their olfactory communication. Fifty hours of field observations confirmed most of the findings in the captive animals.

Four scents are important in the social life of the pronghorn: They originate with the paired subauricular and ischiadic glands, the single dorsal gland and the odour of urine. The subauricular and dorsal scents are produced by males only. Urine is an important component of the sniffing – pawing – urinating – defecation sequence of the males. The ontogeny of this sequence is described. An experiment with an artificial marking post demonstrated that the subauricular scent of a male one rank lower released the strongest response in other bucks. Preliminary gas chromatographic analysis of the subauricular scent has been carried out.

We have undertaken a study of scent communication in the pronghorn (*Antilocapra americana*). A male and a female were raised together in 1969, and two males together in 1970. Both pairs were observed until up to two years of age. Fifty hours of observations of wild pronghorn in the Upper Pahsimeroi, Idaho, and the National Bison Range, Montana, helped us to understand the behaviour of our captive animals better.

The pronghorn uses scent, sound, visual and mechanical communication. Highly developed scent glands serve in scent communication, to which this paper is confined. The males possess pairs of subauricular (postmandibular, or “jaw patch”), ischiadic (“rump patch”), and interdigital (forefeet and hindfeet) glands, and a single mid-dorsal gland, while the females have only ischiadic and interdigital glands. In addition, the urine is of great social importance.

Subauricular scent

The scent of the subauricular gland (located below the ear, Fig. 1) is very potent to the human nose and to the authors it resembles the odour of burnt, fried potatoes. This odour was first noticeable to us in 33 to 35-day old males. The subauricular scent plays an important role in three different contexts: one is a direct confrontation between two individuals, the second is licking of the jaw patch by the female, and the third a depositing of scent by rubbing the gland on plants. The licking by the female has not yet been described in the wild.

In a direct encounter, a buck approaches a male or female slowly, with the head held up, then stops briefly, and throws his head to one side so that the cheek and subauricular gland of one side face the other individual. Hand-raised males approach each other and humans (Fig. 2) in this way, and a sudden wave of strong odour can be noticed. This behaviour pattern occurs most frequently during courtship when bucks approach does in this fashion (Fichter, pers. comm.). Hand-raised bucks regularly approach humans this way before trying to mount. In male-male encounters this behaviour pattern causes the other individual to withdraw.

Our hand-raised female started to lick the jaw patch of her 2-day-old “sibling” when she was 5

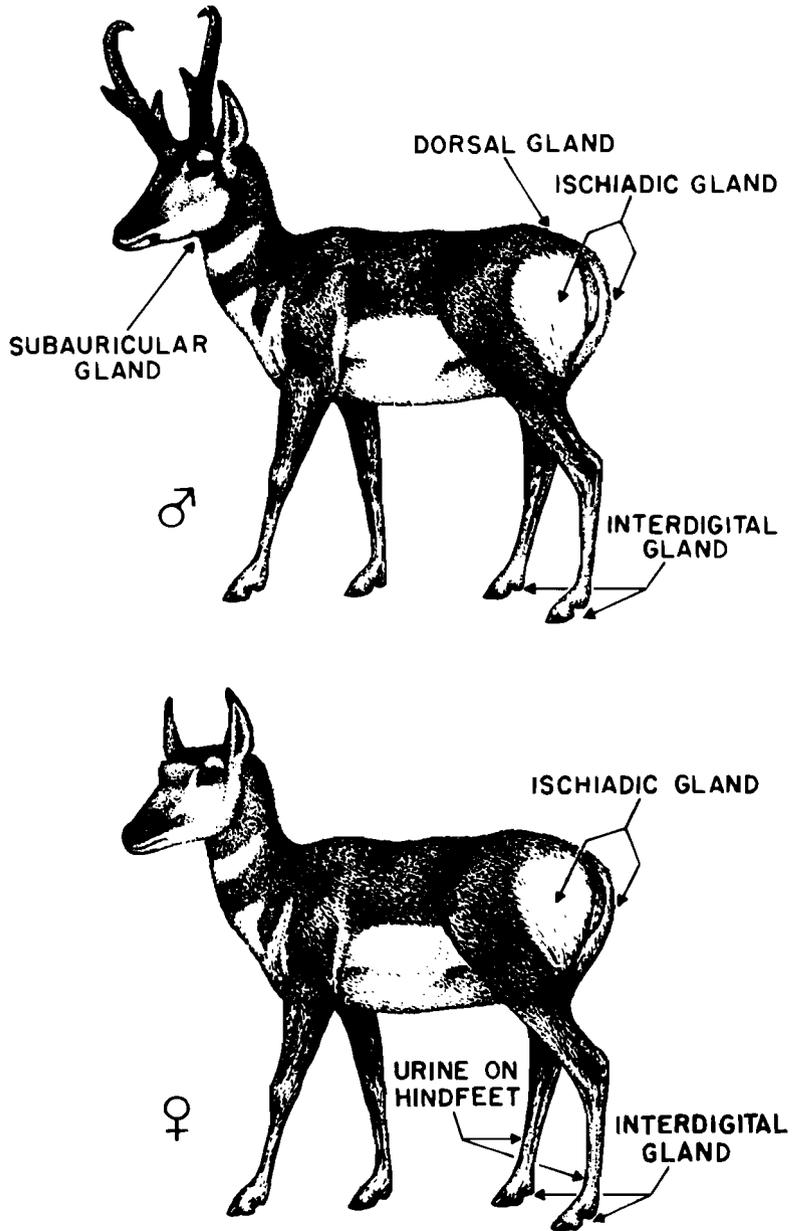


FIGURE 1

The most important sources of social scents in pronghorn. Top: male, bottom: female.



FIGURE 2

A yearling buck turning the head and showing the jaw patch when courting a person.

days old. We observed the same female licking the buck's jaw patch when they both were yearlings and again as two-year-olds. This occurred in both years during August and September which mark the height of the rutting season. The male then holds his head motionless. It should be noted that mutual licking does not occur as a regular pattern in pronghorn as it does in deer.

The rubbing of the "jaw patch" on plants such as sage (*Artemisia*), mullein (*Verbascum*), or thistles has often been observed. It occurs primarily in territorial males (Bromley, 1969) and most often in the rutting season (Prenzlou *et al.* 1968), but also in bachelor groups. In late July, at the National Bison Range in Montana, territorial males rubbed their jaw patches on plants 11 times per hour on the average. Our captive two-year-old and the two yearling bucks rubbed their jaw patch frequently on the gate, chokecherry bushes (*Prunus melanocarpa*), and plants such as mullein (*Verbascum*) and sunflowers (*Helianthus*).

The significance of this type of scent marking, however, has remained obscure. The scent may serve as a deterrent to intruders, as a guidepost to females or the territory owner or simply as information about the males in the vicinity. In bachelor herds, subtle dominance relationships between males may be affected.



FIGURE 3

Two-year-old buck rubs the jaw patch at a marking post.

For a quantitative study of subauricular marking we used an artificial marking post consisting of a vertical metal pipe and a 30 cm long teflon crossarm (Fig. 3). In one experiment we tested whether our three captive males distinguished the subauricular scents of absent individuals. One two-year-old buck was put into a pen by himself. One end of the teflon rod of the marking post (cleansed first with hot water and detergent, and then acetone) was rubbed on the buck's jaw patches and then placed in the center of the pen. The post was left in the enclosure for 15 minutes and then replaced by a new one again rubbed against the buck's jaw patches. The same was repeated a third time. After these three exposures to "own scent" the subauricular scent of one of the yearlings was presented three times in the same fashion, and finally that of the other yearling. This amounted to nine sequential exposures to subauricular scent samples, three from each male. The following day, one of the yearlings (ranking second after the two-year-old buck) was put by himself in the pen and tested in the same fashion, starting with his own scent. Finally, the third-ranking yearling was exposed to nine odour samples, with his own subauricular scent first.

The frequency of the four most typical behaviour patterns were recorded. These were sniffing, licking and chewing, jaw patch rubbing, and thrashing with the horns (Tables 1 to 3). The experiment demonstrated that: a) each male licked and ingested the deposited material (as we had observed before in the female); and b) each male reacted most strongly to the subauricular odour

TABLE 1
FREQUENCIES OF JAW PATCH RUBBING BY THREE PRONGHORN BUCKS IN
RESPONSE TO SUBAURICULAR SCENT OF EACH MALE

Rank of buck	Scent Donor			Total	Significance of distribution (X^2 test)
	1	2	3		
Responding buck	1 ..	21	39	18	$p < 0,01$ NS
	2 ..	0	2	2	
	3 ..	0	0	0	
Total	21	41	20	82	

TABLE 2
FREQUENCIES OF THRASHING BY THREE PRONGHORN BUCKS IN RESPONSE
TO SUBAURICULAR SCENT OF EACH MALE

Rank of buck	Scent Donor			Total	Significance of distribution (X^2 test)
	1	2	3		
Responding buck	1 ..	7	10	8	$p < 0,001$ NS
	2 ..	3	6	15	
	3 ..	1	0	1	
Total	11	16	24	54	

TABLE 3
FREQUENCIES OF SNIFFING AND LICKING OF THREE PRONGHORN BUCKS IN
RESPONSE TO SUBAURICULAR SCENT OF EACH MALE

Rank of buck	Scent Donor			Total	Significance of distribution (X^2 test)
	1	2	3		
Responding buck	1 ..	36	64	46	$p < 0,025$ $p < 0,001$ NS
	2 ..	26	21	61	
	3 ..	14	18	28	
Total	76	103	135	314	

of the one just below him in the social rank order. This applies to both the agonistic behaviour (thrashing and rubbing, Tables 1 and 2) and the investigative behaviour (sniffing and licking, Table 3). The consistently stronger responses to the odours of other males are the more remarkable as they followed "own odour" which came first in each series, and habituation would be expected to take place with repeated stimulation.

Gas chromatographic analysis of the subauricular scent

Analysis of some scent samples extracted from subauricular hair of bucks shot in the wild showed two main peaks (A and H in Fig. 13). The general pattern of these peaks is simpler than, for instance, that of the tarsal scent in black-tailed deer when analyzed under the same conditions (Brownlee *et al.* 1969; Müller-Schwarze 1971). For our investigation of the individual variability of the scent, 200 to 320 mg hair was shaved from each captive buck, and the scent was extracted and distilled. Peaks B through G are too small for quantitative comparisons in the chromatograms for each individual (Fig. 13). Peaks A and H, however, vary in absolute and relative size. Peak A is smaller as measured in the sample from male 2, and peak H is larger in the sample from male 3 than are the comparable peaks for the two other bucks. The smallest amounts of A and H are found in the sample from male 2, and the largest in the sample from male 3. Fractionation, with the ultimate goal of chemical identification of the behaviourally important compound(s), has commenced. Peak A has the typical jaw patch odour. It should be noted that further fractionation typically shows that a "peak" consists of more than one chemical substance.

**FIGURE 4**

The dorsal gland area shows in the fur of a day-old male.



FIGURE 5
Female yearling licks dorsal gland of male yearling.

The scent of the dorsal gland

Located on the mid-dorsal line anterior to the tail base, the dorsal gland (or "supracaudal gland", Schaffer 1940) has been described several times (e.g. Moy 1971). The odour of the fatty secretion resembles that of the jaw patch and is noticeable to humans in males 6 to 8 days old. Its function is unknown. The dorsal gland area is visible as a furless spot from birth (Fig. 4). At the age of 8 days the female started to lick the dorsal gland surface intensely and the surrounding hair of the male raised with her. Her interest in the dorsal gland is still strong, now that she is adult (Fig. 5). Males rarely pay any attention to their own dorsal gland or that of another male. If the licking proves to be a regular pattern in this species, it could possibly provide the females with a "priming" pheromone.

The males erect the hair around the dorsal gland and thus enlarge the odour carrying surface immediately prior to and during copulation (Fig. 6), when thrashing, during play, and when sniffing or eating choice food such as newly presented fresh alfalfa or apples (Fig. 7), or when sniffing piled up wood or wire brought into the pen. In the National Bison Range, males raised the dorsal gland hair while herding the females, when threatening or chasing another male, and in



FIGURE 6

The hair around the dorsal gland is erected during an attempt to mount a person behind the fence

subtle encounters within an all male bachelor group. Because of this variety of circumstances, at the present time it is very difficult to define a state of the animals which is common to them during activation of the dorsal gland.

The ischiadic scent

The ischiadic glands are located on either side of the tail in the large white rump patches (Fig. 1). The smell is reminiscent of buttered popcorn and seems to be the same in both sexes. The organ is primarily composed of sudoriferous glands (Moy 1970). Ischiadic scent is discharged in a brief puff before and during flight. It therefore falls into the category of alarm pheromones. The long white hair of the rump patches is raised as the scent is discharged, thus providing a visual as well as chemical signal. Buechner (1950) described the "strong musky odour" and the "yellowish fluid exuding from the glands" in several shot pronghorn specimens.

Odour produced by the ischiadic glands was noticed in fawns that were 6 to 8 days old – simultaneously with the appearance of the dorsal scent in the males. Also, at 5 days of age males



FIGURE 7

A male fawn erects hair around dorsal gland when eating apples.

began to sniff the rump patches of others, and the rump patch of five-day-old males was sniffed by other males and by the female for the first time.

The rump patches serve as a visual signal very early in life. The captive fawns flared their white patches when following the caretaker as early as the first day of life. On the second and third day they spread the long white hair only when walking away from the caretaker and/or to their sleeping site (Fig. 8). We infer from these observations that, in the wild, the rump patches of the fawn serve as an important visual stimulus for the mother.

When the female was 8 days old she flared her rump patches when sniffing the sleeping site of the 5-day-old male. She sniffed the ischiadic gland of the male repeatedly; and her rump patches were licked intensely by the male. At the age of 14 days she flared the rump patches when most distant from the bedding site and the caretaker.

When placed in a new pen, the male (17 days old) and the female (20 days old) sniffed each other's ischiadic glands. On her 20th day of life we noticed for the first time that the female gave off ischiadic odour when escaping.

When 23 days old, the male started to sniff the rump patches of the female before mounting her. The sniffing of rump patch and tail area typically preceded mounting in all observed animals.



FIGURE 8

Two-day-old fawn flaring rump patches when walking away from caretaker.

Urine in connection with pawing and defecation

As in most terrestrial mammals, urine is utilized for scent communication in the pronghorn. The males go through an elaborate and rigid sequence of sniffing the ground, pawing, urinating on the pawed spot, and finally bringing the hindlegs forward and defecating on the urine (SPUD sequence, Figs. 9-11). After sniffing female urine on the ground, the males may show the "Flehmen" response, in which the head is held forward and motionless, the upper lip is lifted, and air is inhaled and exhaled rhythmically (illustrated in Fig. 12). Then the sequence is SFSPUD or SPFUD. The SPUD sequence occurs in the wild at traditional sites (Fichter, personal communication). In captivity it is also seen at certain points close to gates that are used over and over again. The SPUD of one male has a facilitating effect on the other males. Frequently all three of our tame males perform the SPUD immediately following one another.

The SPUD also occurs in response to novel stimuli, such as alfalfa (*Medicago*), grass, or catnip (*Nepeta cataria*) brought into the pen. If these materials are distributed in several piles over the pen, the two-year-old buck may perform the SPUD at several heaps within a few minutes. He may run out of fecal pellets, but there seems to be always enough urine left for another display. The ritualization of that marking behaviour has evidently reached a degree at which even the emptying of the bladder has been modified in the service of a social marking function.



FIGURE 9 - 11

Two-year-old buck sniffs and paws, urinates, and defecates (SPUD sequence).



FIGURE 12
Yearling male during Flehmen. Note that horns have just been shed.

We have found the following stages to characterize the development of the male's responses to urine leading to the SPUD (ages given refer to earliest appearance of each stage in any of the males):

1. Urination without prior stimulation by the mother or caretaker occurs first at the age of 3 to 4 days.
2. Urinating on the ground and lying down on it (6th day of life).
3. Sniffing of own urine on the ground (8 days).
4. Distance attraction and social facilitation: one male goes to another male that is urinating and urinates in the same area (8 days).
5. Licking of urine (14 days).
6. Sleeping site soaked with urine (14 days) and unrest after removal of that urine (15 days).
7. Urination and defecation simultaneously when being grabbed (18 days).
8. Attraction to and examination of urine, social facilitation and ingestion of urine: one male goes to a urinating male, sniffs the urine, urinates in turn, and 15 minutes later sniffs and eats the urine-soaked soil (34 days).
9. Approach urinating female, sniff urine and stand immobilized (37 days).

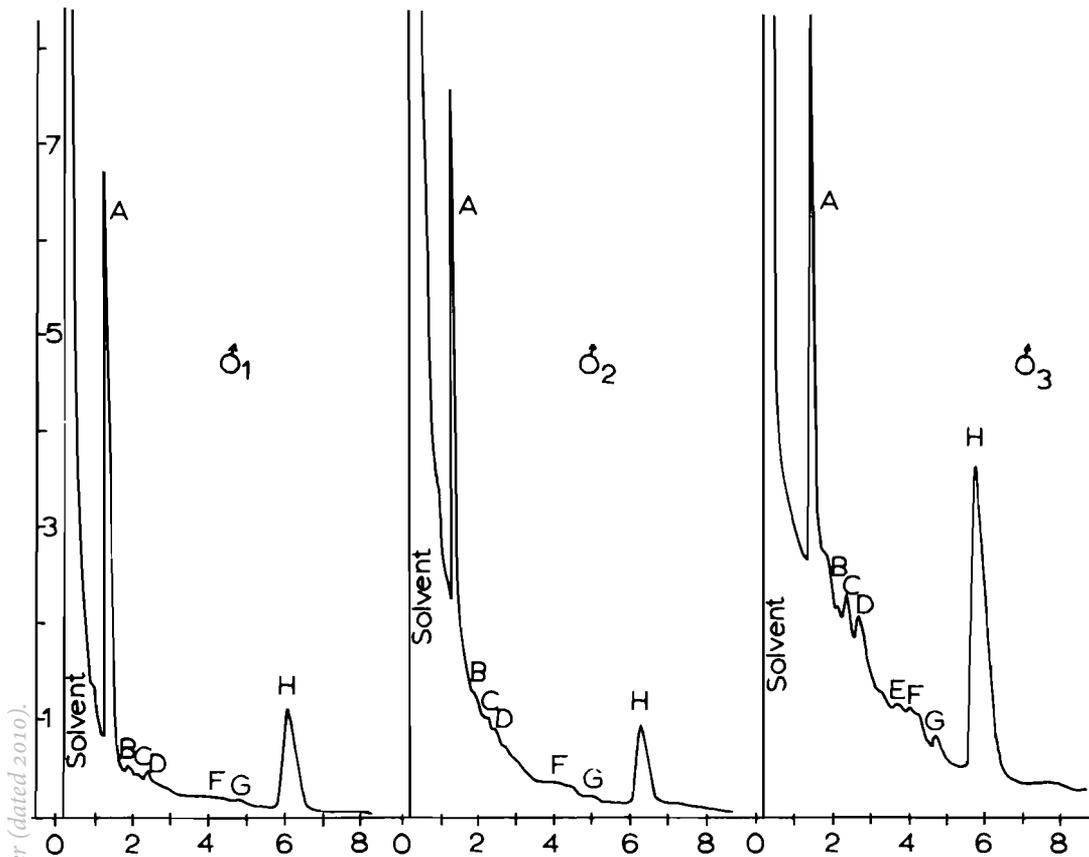


FIGURE 13

Gas chromatograms of the subauricular scent of three males. δ_1 : 2-year-old, δ_2 and δ_3 : yearlings. Abscissa: retention times in column in min. Ordinate: pen deflection: 10 = full scale (1 mV). A - H: peaks used for quantitative comparisons. Column: 15% FFAP, 1,5 m long, 2,4 mm I.D. Temperature: 200°C.

10. Urinating and defecating temporally correlated (UD sequence) without moving hindlegs forward before defecation (42 days).
11. Site tenacity: use of same spot for repeated urination and defecation (42 days).
12. Hindlegs brought forward between urinating and defecation (complete UD sequence, 44 days).
13. Approach to urinating female and urinating in turn (55 days).
14. Flehmen (Fig. 12) in response to female urine (6 months), in response to (own) male urine (8 months).
15. Pawing started to precede urinating at 6 months of age. First pawing occurred in response to male urine in sequence SPSFUD, and in SPSFUD response to female urine.
16. Male urine on the ground releases SPUD in proper temporal sequence, but poorly localized

(6½ months): a male approaches a urinating male, sniffs his urine, paws, goes one step forward, urinates on a separate spot, goes two steps and defecates so that the two urine spots and the feces are all at different sites, and not on top of each other as in the complete SPUD in mature bucks.

At 6½ months of age, another male also sniffed the urine of a yearling buck, pawed, performed Flehmen, went one step forward, urinated on top of the other male's urine, but defecated while walking away. This non-localized defecation is the typical female pattern (Fichter, pers. comm.).

17. UD performed next to urine of female (8 months).
18. The complete and well localized SPUD started to occur regularly when the males were one year old. It should be noted however, that the male which was raised together with the female first showed the full SPUD when he was two years old. He had been together with the other two males from the age of 15 months on. His first SPUD occurred in response to a small *Verbascum* plant not extending above ground level.

Considering the developmental stages, it is obvious that the urine is the element in the complex sequence which provides the olfactory stimulus for the SPUD, especially the pawing, which seems to be the most stimulus-dependent component. Pawing may also vary considerably in intensity and is perhaps linked to the aggressive state of the animal. Also, it is possible that experience with SPUD sites of other males is essential for the development of the SPUD in a young male.

At this time we do not know the exact information conveyed to conspecifics by the SPUD, but it occurs in response to certain social contexts. For instance, our two-year-old male performs the SPUD at the fence when the familiar caretaker approaches or moves away through the adjacent pen. It is often not connected with aggressive behaviour; upon entering the enclosure, the caretaker is courted instead.

Urine on hindlegs

The female and the males, before the age of one year, regularly urinated on the anterior side of their toes and metatarsi. These then emitted odour and were dark brown in color. In one male and the female we first noticed the accumulation of urine on the hindfeet at the age of 4 months. Repeatedly, we observed mutual sniffing of these urine deposits. It is not clear at this time what function the urine serves in this context. Traces may be left on the vegetation through which the animals walk. Gilbert (personal communication) observed urine stained hindfeet of mature female pronghorn in the wild in Yellowstone National Park. We never saw responses to the interdigital glands.

Environmental odours

When capturing newly born fawns in the Idaho sage desert, a 24 hour-old male fled from us. He ran about 400 m in a circle to return precisely to the same spot where he had been bedded before. This remarkable orientation ability raises a question about what cues the animal uses.

While for long-range orientation, visual stimuli probably are important, the sense of smell seems to serve in short-range orientation. One of our four hand-raised fawns found its sleeping site at the edge of a lawn by slowly sniffing along the taller plants bordering on the lawn.

Very peculiar behaviour occurs in response to novel plant odours. After sniffing materials such as crushed grass, rotten apples or the cud of deer, pronghorn of both sexes move their lips rhythmically at a rate of 150/minute for a long period, sometimes for longer than 20 minutes. During that period they may show interest in food, such as alfalfa or apples, but are unable to eat. When put in the mouth the food falls out again. The motor pattern differs clearly from the slower, but more intense smacking of the lips by bucks prior to copulation (Müller-Schwarze and Müller-Schwarze 1970).

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