Lip-Smacking in the Pronghorn (Antilocapra americana)

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This paper describes a peculiar behavior pattern of the pronghorn (Antilocapra americana) that seems to be unique among mammals.

Animals: In 1969 and 1970 we raised a total of three males and one female pronghorn that we had collected in the Upper Pahsimeroi in the Idaho sage brush desert. The young pronghorns ranged in age from a few hours to three days at the time they were taken from the field.

Description: All individuals were repeatedly observed sniffing an object intensely and then moving the upper and lower lips vertically and rhythmically. In addition, the tongue and the lower jaw move up and down in the same rhythm, while the teeth are bared (Figs. 1 and 2). Sometimes, when close, we could hear the lips smacking.

The frequency of the lip movements varied. One male fawn smacked his lips 72, 80, and 92 times per minute during one period. On another occasion we counted 200, 148, 180, and 140 times/min for one male fawn and 184, 180, 208, and 160 times/min for another of the same age. The average for all these 11 frequencies is 149.5 ± 46.1. By comparison, two male fawns chewed their cud at a rate of 137.3 ± 3.4 times per minute. The young pronghorns continued to move their lips in the described manner.
for 8–21 min (average 14.9 ± 4.0) without interruption.

The most remarkable fact about this behavior pattern is that it cannot be "turned off" for sometime. Once "turned on", a hungry animal may be confronted with a milk bottle or other desired food, such as alfalfa or apple, and it may show keen interest in the offered food, but is unable to eat. This peculiar behavior has not been described from the wild. E. Fichter (per. comm.) observed an "oscillating of the upper lip" in two wild females, while others in the group chewed vegetation. The "oscillating" lasted at least 5 min.

The releasing situation: We have observed lip-smacking 28 times. In seven cases, the releasing stimuli were unknown. Of the remaining 21 cases, three occurred after prolonged sniffing of crushed plants (grasses and genus Lactuca) on the ground; three were in response to plant material on the soles of the shoes of the caretaker; three were responses to bitten and chewed grass or alfalfa stems still standing; two were to regurgitated cud of a female mule deer (Odocoileus hemionus hemionus) in the same pen; and seven were occasioned after intense sniffing of fresh diarrhoeic droppings — with the odor of cud — of female black-tailed deer fawns (Odocoileus hemionus columbianus) in the same pen. Once a yearling female started lip-smacking after sniffing a rotten apple. The two remaining incidents occurred after a male was exposed to the scent of its own subauricular gland ("jaw patch"), and after another male thoroughly sniffed the surface of freshly painted furniture. There are 19 responses to plant material in various forms and only two to other odors. A chi-square test — with Yates' correction for continuity ($x^2 = 12.8; p < 0.001$) — shows that we can justifiably conclude that lip-smacking is a response to plant materials. It probably is connected with feeding behavior. Lip-smacking was never observed in a social, sexual, aggressive, or alarm context. The sense of taste does not seem to be involved, as the animals did not smack their lips when licking salt for the first time.

Usually an individual responded to the same kind of stimulus only once or twice with lip-smacking. Even though the particular stimulus, such as crushed plants in the pen, or plant materials on the shoes of the caretaker were present every day for several months, these situations would only initially release the lip-smacking behavior.

Ontogeny: In three males the first lip-smacking occurred when they were 15, 18, and 23 days old, respectively. The female showed it first when 13 days old. From then on, the behavior pattern was observed occasionally until the animals reached the age of 1 year and could be considered sexually mature. It seems to occur throughout life.

Relation to other behavior: There are certain types of behavior in captive pronghorns that are precluded as long as the lip-smacking takes place. Such activities as
drinking from the milk bottle; eating solid food, such as alfalfa or apple; licking urine of another pronghorn and performing the Flehmen response afterwards; licking the caretaker followed by the Flehmen response, are all precluded. Those activities which require the participation of the lips, tongue, teeth, or lower jaw are effected. During lip-smacking even a hungry fawn will stand in front of the milk bottle but be unable to take the nipple and drink. This inability may continue for several minutes.

On the other hand, certain other types of behavior may occur simultaneously with lip-smacking. The movements of the lips and lower jaw may continue unabatedly while the animal reclines, sniffs plants, fights with another individual or the caretaker, escapes, mounts another pronghorn, or assumes the alert posture. Often a pronghorn just stands motionless and smacks its lips.

If the lip-smacking interferes with eating responses, the opposite is also true. When the animal is interested in eating soil or in sucking at the milk bottle, for instance, lip-smacking may stop earlier than on other occasions, although it still takes several minutes for the behavior change to occur.

Possible function: The function of lip-smacking as an olfactory response to plant material is obscure at present. The prolonged behavior pattern is visible and audible, therefore, it could possibly serve in communication.

We observed that one individual is attracted to a place where another sniffs and starts to move the lips in the described fashion. Usually, however, the intense sniffing already attracts the conspecific, and both start to smack their lips at about the same time. Because the lip-smacking lasts so long, other individuals, such as mother or sibling, are certain to notice it.

If this behavior is used as a communication signal, the information content would be limited to the message: "individual x has encountered a smell of plant materials for the first time(s)" , because the motor pattern occurs only after initial exposure to certain stimuli. Perhaps lip-smacking does not possess communication value at all. If it occurred very frequently, the animal would be unable to feed for considerable amounts of time. This would certainly be dysgenic for the species. Because of this danger, it may currently be kept to a minimum by selective pressures.

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**Fig. 2.** Lateral view of the head of the same male at the same occasion and at the same phase of lip-smacking as in Fig. 1.
Similar movements, also called lip-smacking, in other mammals are difficult to compare, because the form and function are different. Black-tailed deer males smack their lips during rutting season when approaching a doe, particularly one that is reclining. According to our observations, this seems to reduce the chance of the doe fleeing. Similarly, social attraction appears to be the major underlying factor in the lip-smacking of primates (van Hooff, 1962). It occurs in a number of species of Macaca, Papio, Cercopithecus, and others. In Papio ursinus, lip-smacking precedes copulation and lasts during the act (Bolwig, 1959). Lip-smacking in primates is also much faster than in the pronghorn; van Hooff reports seven smacks per second on the average.

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Summary
A behavior pattern in the pronghorn (Antilocapra americana) is described for the first time. Lip-smacking occurs after intense sniffing of novel plant odors. Lip-smacking lasts often over 20 minutes and interferes with other mouth-connected behaviors, notably feeding responses. The function of lip-smacking is unknown.

Zusammenfassung

Literature

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