REFERENCES

FOREHEAD GLANDS IN WHITE-TAILED DEER

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ABSTRACT.—Skin biopsies were taken from the forehead of adult female and adult male white-tailed deer during the sexually quiescent season and again during the rut. Samples were also taken from the same and other locations on freshly killed animals of both sexes and ages 6 months to 9+ years. Microscopic examination revealed large numbers of tubular apocrine sudoriferous glands relative to the integument in general. During summer, glands of both sexes exhibited little activity. In the rut, glandular activity was moderate in females and very high in males, which is consistent with the annual testosterone cycle. Activity was highest in dominant males and lowest in fawns. This and other evidence indicate that the forehead is a scent organ used to anoint antler rubs made by males during the rut.

During the fall, male white-tailed deer (*Odocoileus virginianus*) make visible markings on saplings called "antler rubs." Rubbing was long thought to serve only to clean and polish antlers or as practice combat. Antler rubbing in early fall undoubtedly has some of these functions, but Kile and Marchinton (1977) found that rubs continue to be made throughout the breeding season (rut) and that these later rubs differ physically from those made during antler cleaning. Deer are occasionally seen sniffing and licking rubs, and Moore and Marchinton (1974) demonstrated that scent is left on them. The role of rubs in the social life of deer is a matter of conjecture, but we presume they serve as scent posts and function in breeding behavior (Marchinton and Hirth, in press).

The source of the scent associated with rubs has never been identifed. The forehead region has been shown to have a scent-producing organ in roe deer, *Capreolus capreolus* (Schumacher, 1936) and muntjac, *Muntjacus reevesi* (Barrette, 1976). The white-tailed deer lacks the obvious external structures that these cervids possess, but our field observations suggest the forehead of *O. virginianus* is also a source of marking scent. The black-tailed deer (*Odocoileus hemionus columbianus*) makes similar signposts (Müller-Schwarze, 1971, 1972), and Volkman et al. (1978) found that it responds to "artificial branches" rubbed on the forehead of conspecifics. Quay (1959) studied the cutaneous glands of white-tailed deer, but did not examine the forehead. Quay and Müller-Schwarze (1970, 1971) studied the skin glands of black-tailed deer and mule deer (*O. h. hemionus*), but found little evidence of glandular activity in the forehead of either subspecies. We hypothesized that the forehead of white-tailed deer does function as a scent-producing organ, and our objectives in this work were to (1) describe the histological structure of the forehead skin, and (2) measure the seasonal, sexual, and age variation in activity of the glands of this area.

METHODS

Four adult female and four adult male white-tailed deer were selected from our captive herd of semitame animals. A skin biopsy was taken from each animal during July and again from the same individuals during the height of the rut in November. Deer were anesthetized, a part of the forehead shaved and scrubbed, and a 3.0 by 0.5 cm section of skin was taken along a line from the antler pedicel (or corresponding spot on does) forward to the midline of the skull and intersecting it at 45°. The incisions were closed with sutures and the animals monitored until healed. Additional samples were obtained from 11 live or freshly-killed wild deer of various ages. These samples were taken from the forehead, side of face below eye and ear, midline of neck behind ears, and back.

Skin samples were fixed, processed, and sectioned with standard histological techniques and stained with hematoxylin and eosin. The slides were numbered to conceal the identity of the animal from the observer, and were examined to provide a general description of the tissue and to determine the level of activity of the sudoriferous glands.

Actively secreting sudoriferous glands are distinguished from inactive ones by thicker secretory epithelia in the basal portion of the glands and by apical projections on the epithelial cells. We quantified the degree

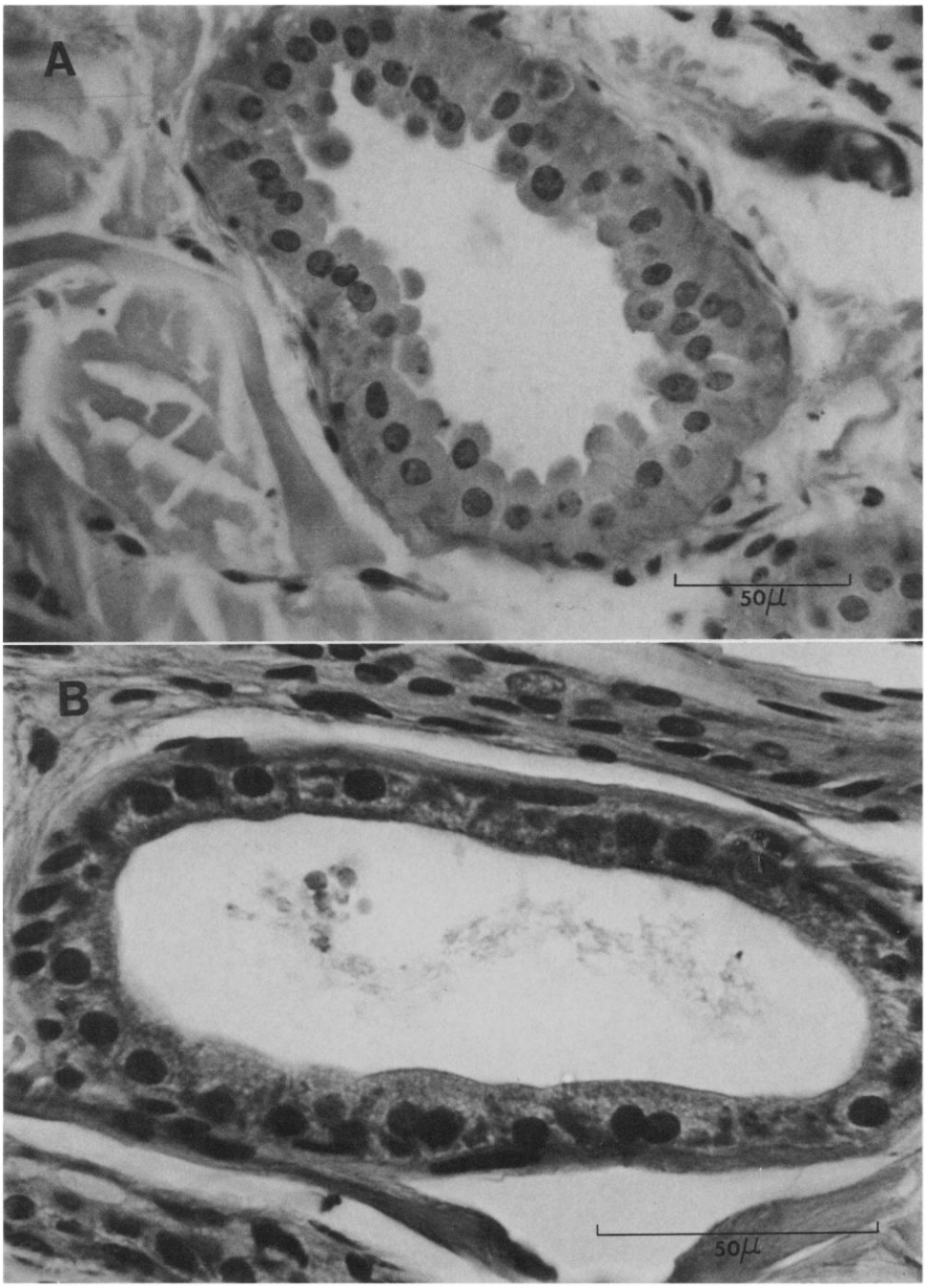

FIG. 1.—Cross-sections of secretory tubules of active (A) and inactive (B) apocrine sudoriferous glands from forehead of adult male *Odocoileus virginianus* taken from rut and non-breeding season, respectively.

TABLE 1.—*Degree of activity and thickness of secretory epithelium of sudoriferous glands from eight white-tailed deer during summer and rut.*

Deer	Sex	Age	Proportion (%) of active glands		Thickness of secretory epithelium (μ) ($\bar{X} \pm SE$)	
			Summer	Rut	Summer	Rut
551	F	4	3/135 (2)	48/80 (60)	8.0 ± 0.4	17.3 ± 1.0
600	F	3	8/87 (9)	14/115 (12)	9.5 ± 0.6	14.5 ± 0.6
589	F	3	2/126 (2)	23/103 (22)	9.1 ± 0.4	16.1 ± 1.1
507	F	2	4/106 (4)	6/76 (8)	8.5 ± 0.4	17.0 ± 1.6
599	M	5	3/116 (3)	210/235 (89)	9.1 ± 0.7	33.1 ± 1.2
76	M	3	17/107 (16)	169/175 (97)	13.8 ± 0.7	29.5 ± 1.1
506	M	3	7/95 (7)	105/130 (81)	10.8 ± 0.7	26.3 ± 2.0
555	M	2	50/53 (94)	77/77 (100)	20.5 ± 0.5	37.7 ± 1.4

of enlargement of these cells by measuring the thickness of the secretory epithelium. For every animal, 20 glands were selected systematically on two different slides from each season and measured with an ocular micrometer. In addition, we examined every gland on two slides for the presence of apical projections to obtain an estimate of the proportion of active glands for each animal.

RESULTS

Histology.—The forehead region had many large hairs which, upon assumption of winter pelage, gave the head of the male a distinctive appearance. The skin of the forehead was thickened and possessed large amounts of fibrous connective tissue relative to other areas about the head and neck, particularly in males during rut. The arrector pili muscles were similar to those on the body in general as were the sebaceous glands with respect to both size and number.

Of particular interest were tubular apocrine sudoriferous glands (Fig. 1), which terminated inside the opening of the hair follicle above the sebaceous gland. These glands were numerous and well developed in comparison with those in samples taken from elsewhere on the head and neck, but were not as numerous or developed as those described by Quay (1959) in the tarsal and metatarsal glands.

Activity of sudoriferous glands.—Analysis of variance of the influence of sex and season (repeated measure) was computed for the thickness of the secretory epithelia (Table 1). Males had thicker secretory epithelia than females ($P < 0.01$), but during the rut they were relatively thicker in both sexes than during summer ($P < 0.01$). There was a significant interaction between sex and season ($P < 0.01$), however, which implies that much of the difference between sexes came from the considerably greater thickening shown by males in rut and not from a difference between the sexes in summer.

Tests for differences in the proportion of active glands were made using two-way tests for association in contingency tables. Males ($P < 0.01$) and females ($P < 0.01$) were found to exhibit increased levels of glandular activity during the rut. The glands of males were significantly more active than those of females both during the summer ($P < 0.01$) and rut ($P < 0.01$). We made no quantitative comparisons between deer of different ages, partly because of limited samples in each age class, but also because the rudimentary state of the glandular development of fawns prohibited scoring by the same criteria used for adults.

DISCUSSION

The forehead pelage of mature male white-tailed deer is markedly different in color and texture from that of does. This is especially evident during the rut when appearance of the forehead alone is sufficient for a perceptive observer to identify the sex. Our study provides evidence that this sexually dimorphic portion of the skin serves as a scent-producing organ that functions in signpost communication during the breeding season. We feel we have three lines of evidence.

First are our observations of the manner in which bucks make rubs. They lick and nuzzle the bole of a small tree and vigorously rub it vertically with the antlers. Most of the rubbing motions are made with the basal medial portions of the antler beams and with the forehead itself. Many lay observers and some biologists have assumed the scent associated with rubs comes from the pre-orbital glands, which are conspicuous and are used for marking by some ungulates. Our observations contradict this. White-tailed deer may use the pre-orbital glands in other behavioral contexts, but in making rubs they show none of the deliberate use of the pre-orbital area as is characteristic of species, such as Eld's deer, *Cervus eldi* (Müller-Schwarze, 1975; Blakeslee et al., 1979), and muntjac, *Muntjacus reevesi* (Barrette, 1977), for which use of these glands has been established.

Second, sebaceous and apocrine sudoriferous glands are the two types that are most often responsible for the secretion of semiochemicals (Quay, 1976). Although sebaceous glands of the forehead are not different from those of the rest of the integument, the apocrine sudoriferous glands are increased in number and degree of development relative to the body in general.

Third, the differences in apocrine sudoriferous glandular activity and development between sexes and seasons are consistent with their postulated function as scent glands. During the summer when sexual activity and antler rubbing are nil, the forehead glands of both sexes exhibit little activity. With the onset of rut, however, the apocrine sudoriferous glands of adult males hypertrophy and become very active, whereas those of females develop only a moderate degree of glandular activity.

The physiological basis for seasonal fluctuation in glandular activity is readily inferred from the literature. Apocrine glands are frequently under hormonal control, with gland development promoted by androgens (Ebling, 1976). Plasma androgen concentrations in male white-tailed deer are low during the sexually quiescent seasons and begin to rise during fall coincident with the shedding of velvet (Mirarchi et al., 1977) and onset of antler rubbing. The highest androgen levels, rut, and forehead sudoriferous gland activity are concurrent.

Our data indicate that in males greater age and possibly higher social status are correlated with increases in forehead gland activity, although these two variables are not independent. Male fawns rarely participate in breeding and did not exhibit glandular activity in the fall. Each of the two groups of penned deer available to us was dominated during the fall by an old male (5+ years) and both dominants possessed the highest level of glandular development. A hunter-killed male, however, that was only 2.5 years old had forehead integument equally as active as that of the much older dominants in our pens. This animal was from a population in which bucks were heavily harvested and it can be assumed that he was involved in breeding and very likely a social dominant. This indicates to us that, although young males generally have less active glands than older ones, the position of an adult male in the social hierarchy is reflected in the level of activity of his forehead glands.

Social position is known to influence marking frequency in many species (see reviews by Ralls, 1971; Johnson, 1973), including white-tailed deer (Moore and Marchinton, 1974). Furthermore, dominance has been positively correlated with size of the ventral scent gland in the gerbil, *Meriones unguiculatus*, (Thiessen and Yahr, 1977), a finding that fits our data and a correlation which may be common. Contrary to earlier work, however, social dominance is not correlated with androgen levels in a variety of species (Lincoln et al., 1972; Gordon et al., 1976; Selmanoff et al., 1977). Rather, androgens have a threshold effect on male behavior; when present at the threshold titer males behave normally, but, within physiological norms, higher levels do not enhance social status. Thus, our limited data on the interaction of social position and development of forehead scent glands concur with other lines of evidence, but the hormonal mechanism underlying this phenomenon remains obscure.

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