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Morphology of the white-tailed deer tarsal gland

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The communication of reproductive information in cervids is thought to be accomplished by odors associated with skin glands. The tarsal glands of white-tailed deer *Odocoileus virginianus* (Zimmerman, 1780), in particular, are the focus of many breeding behaviors and appear to attract the interest of conspecifics. These glands are annointed with urine with increasing frequency as the breeding season approaches and may convey social odors relating to dominance, reproductive condition, or individual recognition. We collected tarsal glands from male and female white-tailed deer of various ages during the breeding and non-breeding seasons. Using light microscopy, we examined skin biopsies of tarsal glands microscopically to quantify sebaceous and apocrine glandular activity. Measurements of sebaceous and apocrine glands did not differ between sexes or seasons, or among age classes. During the breeding season, the tarsal tufts of older males become darkly stained. Although the tarsal glands of white-tailed deer are important in conspecific communication, the staining and associated odors appears to be unrelated to variations in the sebaceous or apocrine gland activity. Rather, odor production on the tarsal gland likely results from interactions among urinary constituents, microbial decomposition, and glandular secretions.

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Introduction

In cervids, skin glands are a source of odors that communicate identity, social status, and reproductive information to conspecifics (Müller-Schwarze 1987). Skin glands typically are stimulated by testosterone and possibly inhibited by estrogens (Ebling 1977). Several species of deer have a raised tuft of hair on the medial aspect of each tarsus. This tarsal tuft and an underlying area of exocrine glandular tissue are collectively called the "tarsal organ" or "tarsal gland" (Müller-Schwarze 1987). Some deer urinate onto their tarsal glands in a behavior called rub-urination. Urine saturates the tarsal tuft and becomes trapped by specialized scent-disseminating hairs (Müller-Schwarze *et al.* 1977, Hoffman *et al.* 1997). These hairs facilitate the

mixing of tarsal glandular secretions and urine, possibly producing unique odors (Müller-Schwarze *et al.* 1978).

Histology of the tarsal region has revealed sebaceous glands, apocrine glands, and erector pili muscles (Quay 1959, Quay and Müller-Schwarze 1970), with sebaceous glands located within the superficial layer of the dermis comprising the bulk of secretory elements. Apocrine glands, a less prominent feature of tarsal gland tissue, are located within a deeper dermal layer and are thought to contribute to the secretions of most mammalian scent glands (Quay 1984). Erector pili muscles of the tarsal gland provide erection of the tarsal tuft. These and possibly other structural components contribute to the overall function of the tarsal gland.

It is difficult to determine if pheromones exist in glandular secretions, urinary products, or both. In male black-tailed deer *Odocoileus hemionus* Rafinesque, 1817, a urinary product is retained selectively by tarsal glands (Brownlee *et al.* 1969). Previously, we investigated the volatile profiles of voided urine (Miller *et al.* 1998) of white-tailed deer *Odocoileus virginianus* (Zimmerman, 1780) and suggested that some volatile compounds from the tarsal gland may arise from microbial decomposition of urinary compounds and glandular secretions.

Functional activity of the tarsal gland may be influenced by age, sex, reproductive status, and social rank, as well as season and other variables. Determination of the relative contribution of glandular secretions and urinary products to tarsal odor production requires an understanding of the various influences on the activity of glandular tissues. Because previous quantification of tarsal tissues in white-tailed deer *Odocoileus virginianus* has been limited to a few animals collected during one season (Quay 1959), we evaluated the influence of age, sex, and season on the activity of apocrine and sebaceous tissues associated with the tarsal gland of the white-tailed deer.

Methods

We obtained tarsal glands from 52 male and 58 female white-tailed deer in the Piedmont physiographic region of Georgia between 22 September 1988 and 2 May 1989. We examined tooth replacement/attrition and used the technique of Severinghaus (1949) to place the deer into 1-year-old, 2-year-old, and ≥ 3-year-old age classes. Samples were fixed in 10% formalin for several days, rinsed in water for 24 hrs, and placed in 70% ethanol until processed. Season of collection was recorded as spring (March–May; non-breeding season) or fall (September–December; breeding season). Hair was shaved from the center of each tarsal gland, and a tissue sample (5 mm × 10 mm) removed. The surface of the skin was embedded at a right angle to the cutting surface of a microtome. Nine serial transverse sections were cut from each block. Three sections were mounted per slide and stained with hematoxylin and eosin.

Area of sebaceous glands (μm^2) was measured using Planar Morphometry software (Microcomp Integrated Image Analysis System, Southern Micro Instruments, Inc., Atlanta, Ga.). Five fields of view were selected and examined from each deer. All sebaceous glands were measured in each field of view, and a total sebaceous gland area was calculated for each deer. We examined a subsample of skin sections (24 males, 27 females) to determine apocrine gland characteristics. Apocrine glands were measured with a computer-assisted image analyzer equipped with Data Image Analysis System software (C-squared Corp., Atlanta, Ga.). For each deer, we measured five well-defined apocrine glands

in proximity to an associated hair follicle. Vertical distance from the skin surface to the closest tubule of the apocrine gland (Apocrine Gland Depth) and greatest vertical distance between opposite ends of the tubular portion of the apocrine gland (Apocrine Gland Length) were measured to the nearest 0.1 μm. Area of the apocrine gland (Apocrine Gland Area) was measured to the nearest 1.0 μm^2 by tracing the perimeter of the tubular portion of the gland. Thickness of apocrine secretory epithelium (Epithelium Thickness) was measured to the nearest 0.1 μm at five locations and averaged. The number of apocrine tubular cross-sections with evidence of secretory activity was counted. Glands were considered active if the secretory epithelial cells possessed apical projections. A percentage of relative apocrine gland activity (Percent Apocrine Activity) was calculated by dividing the number of active cross-sections by the number of all cross-sections within the apocrine gland. Treatment effects were tested with analysis of variance (SAS Inst. 1989). When appropriate, data were rank or log transformed to compensate for heterogeneity of variances. Treatment significance was accepted at $p \leq 0.05$.

Results and discussion

Sebaceous gland area did not differ between sexes or seasons, or among age classes (Table 1). Similarly, apocrine gland depth, length, and area; epithelium thickness; and percent apocrine activity did not differ between sexes or seasons, or among ages (Table 2). We observed considerable variability in measurements among individuals. Furthermore, apocrine activity, based on apical projections, was inconsistent among glands of the same tissue sample. For example, one gland would suggest 100% activity, whereas the adjacent gland would suggest 0% activity.

Many potential factors may control the chemical nature of glandular secretions, including gene regulation, cell types and numbers, and androgen receptors. However, the lack of sexual or seasonal dimorphism in glandular activity suggests that important social odors may result from other sources. Instead, these glands may play an accessory role in the production and retention of scent on the tarsal

Table 1. Tarsal gland sebaceous area ($\bar{x} \pm$ SE) for white-tailed deer sampled during the reproductive (fall) and non-reproductive (spring) seasons from the Piedmont physiographic region of Georgia (1988–89). Measurements were taken to the nearest square micrometer (μ^2) at 5 microscopic fields per deer and then summed.

Sex	Age (Years)	Season	n	Sebaceous Gland Area ($\mu m \times 10^4$)
Female	1	Fall	3	3.09 (2.06)
Female	2	Fall	12	3.22 (1.41)
Female	≥3	Fall	18	3.31 (1.75)
Female	1	Spring	4	2.75 (2.50)
Female	2	Spring	7	3.07 (2.56)
Female	≥3	Spring	14	2.97 (1.80)
Male	1	Fall	5	2.87 (3.85)
Male	2	Fall	17	3.21 (1.97)
Male	≥3	Fall	23	2.81 (1.51)
Male	1	Spring	4	3.75 (3.21)
Male	2	Spring	3	4.75 (9.61)

Table 2. Tarsal gland apocrine measurements ($\bar{x} \pm$ SE) for white-tailed deer sampled during the reproductive (fall) and non-reproductive (spring) seasons from the Piedmont physiographic region of Georgia (1988–89). [a] Vertical distance from the skin surface to the closest tubule of the apocrine gland, measured to the nearest 0.1 μm. [b] The greatest vertical distance between opposite ends of the tubular portion of the apocrine gland, measured to the nearest 0.1 μm. [c] Measured to the nearest 1.0 μm² by tracing the perimeter of the tubular portion of the gland. [d] Measured to the nearest 0.1 μm at 5 locations within an apocrine gland. [e] Calculated by dividing the number of tubular cross-sections with apical projections by the total number of cross-sections.

Sex	Age (Years)	Season	*n*	Apocrine Gland			Epithelium	Apocrine
				Depth[a] ($\mu m \times 10^3$)	Length[b] ($\mu m \times 10^2$)	Area[c] ($\mu m \times 10^5$)	Thickness[d] (μm)	Activity[e] (%)
Female	1	Fall	5	2.44 (0.23)	8.56 (1.09)	3.34 (0.71)	11.3 (0.5)	17.5 (9.4)
Female	2	Fall	5	2.56 (0.13)	7.88 (0.75)	3.30 (0.73)	12.0 (1.0)	25.0 (18.9)
Female	≥3	Fall	4	2.59 (0.18)	9.18 (1.00)	3.14 (0.20)	12.5 (0.8)	19.0 (9.1)
Female	1	Spring	4	2.11 (0.14)	6.66 (0.20)	2.91 (0.28)	13.2 (1.4)	46.2 (19.7)
Female	2	Spring	4	2.48 (0.15)	8.21 (0.99)	3.51 (0.41)	17.1 (3.0)	52.0 (17.9)
Female	≥3	Spring	5	2.35 (0.10)	7.15 (0.47)	2.85 (0.52)	12.3 (0.6)	14.5 (14.5)
Male	1	Fall	4	2.56 (0.21)	7.76 (0.50)	2.83 (0.17)	10.8 (0.5)	0.0 (0.0)
Male	2	Fall	5	2.03 (0.41)	8.23 (0.93)	3.62 (0.62)	12.4 (1.1)	5.1 (3.0)
Male	≥3	Fall	8	2.49 (0.20)	9.72 (0.83)	3.82 (0.59)	12.1 (0.8)	22.3 (11.0)
Male	1	Spring	4	1.99 (0.53)	7.58 (0.83)	3.13 (0.34)	12.0 (0.4)	13.8 (8.5)
Male	2	Spring	3	2.41 (0.13)	7.76 (0.03)	3.60 (0.61)	14.9 (3.4)	24.3 (24.3)

tuft. For instance, lipid secretions from the sebaceous glands, when distributed to the tarsal tuft (Hoffman *et al.* 1997), may selectively adsorb fat-soluble urinary constituents and metabolic products of bacterial decomposition important in intraspecific communication (Gassett and Miller 1997, Gassett *et al.* 1998).

The amount of individual variation in our sebaceous and apocrine gland measurements is consistent with results from a similar study of reindeer (Mossing and Kallquist 1981). We agree that, even when a large sample of individuals from a population shows no treatment related glandular change, differences may be evident in another sample or another population. These differences may be related to age, hormonal history, genetic or other factors increasing the size of preexisting gland units (Quay 1984). However, for this group of white-tailed deer, we found no evidence of sex, age, or season-related glandular activity.

During the fall, older males tend to have darker tarsal tufts than younger males or females of any age. The dark color and pungent odor of tarsal glands of dominant males during the breeding season is evident through casual observation (Moore and Marchinton 1974). White-tailed deer of all ages rub-urinate, but the behavior is most common among dominant males during the breeding season (Marchinton *et al.* 1990). Tarsal glands of dominant males also have more species of microbes than those of subordinate males or females (Gassett and Miller 1997). We suggest that darkly stained tarsal tufts are not the result of increased glandular activity, but

rather the result of frequent exposure to voided urine and subsequent bacterial decomposition, or differences in urinary components.

The tarsal glands of deer in the genus *Odocoileus* may relay information on age, sex, and individual recognition, as well convey social status. Volatile profiles of the tarsal tuft (J. W. Gassett, unpubl. data) and voided urine (Miller *et al.* 1998) of white-tailed deer vary among season, sex, and age classes, and frequent rub-urination likely is necessary to maintain semiochemical cues (Sawyer *et al.* 1993). Because we found no age, sex, or season-related variation in the activity of the underlying glandular tissues, we feel that the activity of the glands themselves probably have an ancillary or accessory role in the production of socially significant odors. Although a number of alternate hypotheses exist as to the source of tarsal odors, we feel a likely scenario is that volatile compounds from the tarsal region may result, at least in part, from microbial decomposition of urinary compounds and glandular secretions. This hypothesis is further supported by recent studies in which 18 species of bacteria were cultured and identified from the tarsal tuft that were specific to that region of the animal (Gassett and Miller 1997).

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