Seasonal variations in general activity, behaviour and cutaneous glandular structures in reindeer (Rangifer tarandus L.).

by

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Abstract

The locomotor activity of the reindeer is separated into a diurnal and a nocturnal phase which, in turn, consists of a number of short-term activity bursts. The onset and termination of diurnal and nocturnal activity are largely in synchrony with sunrise and sunset. Since the diurnal phase is longer, total activity is dependent on the photoperiod. Total activity as well as the number of activity bursts is greater in June with continuous daylight than in December with 6 hours daylight. In winter, reindeer spent less time feeding but more time ruminating and resting than in summer. Synchronization between individuals was also greatest in winter. It is concluded that the described changes in the activity pattern are due to an endogenous component and that this component further controls food consumption and energy balance of the reindeer.

Seasonal variations in behavioural patterns are described. Several specific rutting behaviours, sexual and agonostic, emerge in the male during the prerut and persist until after the rut. The preorbital gland is enlarged and secretory activity is evident. The rut is characterized by the sudden appearance of an odour in the breath of mature males followed a few later by a strong odour in the urine. These odours persist for a short time during the most intense period of rut. The amount of androgen rizes sharply and reaches peak concentrations in late September - early October, decreasing thereafter. The described behavioural cues occur with a certain constancy in time in concecutive seasons.

A quantification of the amounts of secretory epithelia in preorbital, interdigital, caudal and tarsal glands reveals that only the preorbital gland is subjected to any seasonal and sexual variation. The apocrine epithelium in this gland is most developed in mature males during the rutting season and seems to be dependent upon the presence of an elevated androgen concentration. The tarsal gland is the least developed gland while the interdigital and caudal glands are more well-developed and structurally complex. Scattered apocrine glands are only developed on the legs, the ventral body, oral angle and in the rump patch.

Key words: Androgen, Cervidae, dermal glands, locomotor activity, olfactory communication, pheromones, photoperiod, reindeer, rut, seasonal variations.

The following papers are included in the thesis and will be referred to by their roman numerals.

I. Eriksson, L-O., Källquist, L. & Mossing, T. The seasonal development of circadian and short-term activity in captive reindeer (Rangifer tarandus L.) Accepted for publ. in Oecologia.

II. Müller-Schwarze, D., Källquist, L. & Mossing, T. 1979. Social behaviour and chemical communication in reindeer (Rangifer t. tarandus L.). J. Chem. Ecol. 5:4 483-517. (Only the parts of the paper that can be assigned to as "seasonal variations" are referred to here).

III. Mossing, T. & Damber, J-E. Rutting behaviour and androgen variation in reindeer (Rangifer tarandus L.). Accepted for publ. in J. Chem. Ecol.

IV. Källquist, L. & Mossing, T. 1977. The distribution of sudoriferous glands in the hairy skin of the reindeer (Rangifer tarandus L.). Acta Zool. 58 65-68.

V. Mossing, T. & Källquist, L. Variations in cutaneous glandular structures in reindeer (Rangifer tarandus L.) Manuscript.

GENERAL DISCUSSION

Seasonal variations in general activity and behaviour

A major feature of mammalian behaviour is the regular alternation between activity and rest. In ruminants this is comlicated by the dialectic between activity and feeding and the following need for a period of rest and rumination, described in (I).

The daily activity of reindeer is divided into a nocturnal and a diurnal phase which in turn are separated into a varying number of short-term activity bursts. Activity is more intense during the day and taken as a whole it therefore exceeds that for the nocturnal phase. Depending on the length of the photoperiod, the number of activity bursts varies from about 4-6 in winter to about 7-9 with continuous daylight in summer. Sunrise and sunset act as "set points" for the onset and termination of diurnal activity. The nocturnal phase, being less pronounced, gradually decreases as night period diminishes and finally disappears. Also, an evaluation of the food intake in December (I Fig. 2) shows that about 45% of the total intake occurs during the daylight period which only accounts for about 30% of the 24 hours. This results in an annual variation in the total activity. Therefore, increasing daylength prolongs activity and decreases the precuspular resting period in a manner described in Fig. 1.

The short-term rhythm as such may result from a changing level of satiation in the rumen in response to food intake and digestion. A simple model for the explanation of the short

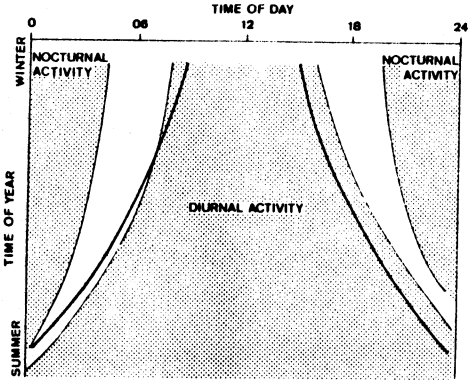

Figure 1. .
The principal changes in the relationships between the photoperiod-, diurnal and nocturnal activities. Thick line indicates the 9-lux threshhold.

term rhythm in the ruminant, not involving endogenous components, could be that the depletion of the rumen causes recurring hunger in turn responsible for the onset of feeding activities. Although the rate of rumen depletion is known to affect this (Bailey & Forbes 1974) one could suspect that other factors are involved and that physiology of the rumen is not the only cause but merely acts by adjusting the pattern of activity. The step may be long between ruminants and small mammals but according to Daan & Slopsema (1978) the common vole (Microtus arvalis) exhibits the usual short-term rhythm irrespective of wether or not food is available, suggesting that the daily variation in feeding motivation is unrelated to the actual acts of feeding and digestion. In the reindeer the activity pattern was determined by the light-dark conditions (I Fig. 3) and although it was subjected to disturbances

in the surroundings the basic pattern was always maintained. From October to December 1976 food was automatically distributed every two hours. The feeding trough was usually visited by the reindeer at the time when food was offered but in spite of this the locomotor rhythm was essentially the same as in 1977 when food was given ad libitum (Fig. 2). From these examples it is quite clear that the regulation of the short-term rhythm is due to an endogenous component and is not caused by factors such as the rate of rumen depletion or the digestability of food.

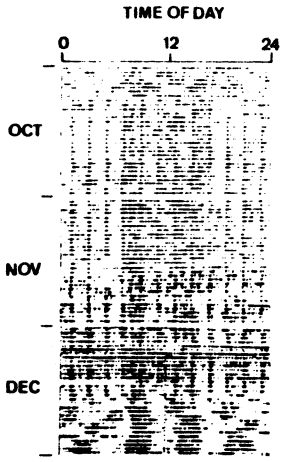

Figure 2.
Activity records of 10 reindeer from October to December 1976. Up to 14 December food was given automatically every 2nd hours, and thereafter ad lib.

Some ecological and behavioural implications follow from the activity pattern of the reindeer and the adaptive significance of this can be taken into consideration. The described activity pattern is the utmost expression of an adaption to a widely fluctuating environment and might well be looked upon as an inherited pattern of a foraging and energy strategy. Annual variations in body weight and energy consumption are known not only in reindeer and caribou (McEwan 1968, McEwan & Whitehead 1970, Reimers, 1972), but seem to be common to most northern species of Cervidae (Wood et al. 1967). Such variations do not occur without correspond-

ing metabolic changes. Moen (1978) describes the annual rhythm of heart rates, activity and metabolism in white tailed deer and explained that "ecological metabolism" was lowest in winter and highest in summer. A reduction of energy demands at times when food is difficult to obtain or scarce is of evident survival value. This is what may be termed a shift between a high cost-high yield method to a cheap but low return foraging method (Krebs 1979, Fig. 2.12). Norwegian wild reindeer spent more time "trotting and running" in summer (and hunting and rutting seasons) than at other times (Gaare et al. 1974). The gradual changeover from low to high activity methods is described in (I) Fig. 6. The duration of activity increased with photoperiod in a 1:1 fashion while an increasing night period only caused an increase of the nocturnal activity in a 0.5:1 relationship. On the other hand, the reindeer spent less time ruminating between meals in June than in September, December and March. Therefore the low-energy winter strategy consists of a low food intake, long resting periods but with a more careful utilization of food; while the strategy for the more hurried summer reindeer is a large food intake with shorter periods of rest and rumination of the ingested, which can assumed to be more wasteful.

The reindeer has two principal ways of responding to the increased energy demands caused by a detoriating environment or by an inherited ability for weight gain. The first way is to increase the meal size. Although calculations of the actual meal size were not performed but food consumption on the whole was about 30% lower in December compared with June. The second

option, and that which actually occurs, is to increase the number of meals or activity periods per 24 hours. This is brought about by the repeated splitting processes of the evening activity burst which causes an increasing number of diurnal bursts of increasingly shorter frequency. This process can simplyfied be described as in Fig. 3.

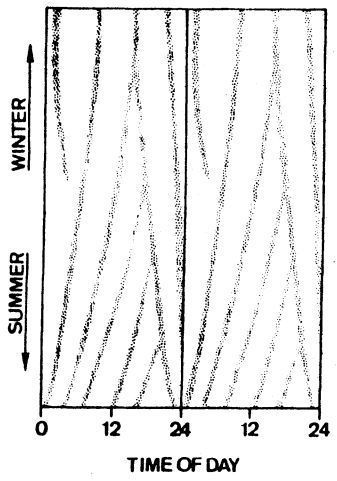

Figure 3.
The changing pattern of short-term activities.

The best way to summarize this could be to describe what the reindeer does not do in response to environmental changes. The reindeer does not compensate for the decrease in diurnal activity by a corresponding increase in nocturnal activity, but instead reduces its entire activity to that of a net energy loss when deposited fats are used. On the whole, this process evidently occurs independently of food availability. Furthermore the change in the light-dark conditions provides the proximate factor for regulating the energy budget by acting on the general activity pattern.

Another effect of the external governing of the reindeer activity is its role in synchronizing activities. A weak or even absent "Zeitgeber" during summer leads to less synchronization and cohesion within the herd. This is also easily

observed in the field. During summer the herd is more loosely organized into subgroups of different size and composition and intergroup activity is less synchronized (Thomson 1973, I Fig. 5). Winter conditions normally causes reindeer to be into larger bands. Although other factors are involved the changing light-dark conditions undoubtedly either help or complicates the cohesion of the herd.

The described activity pattern was obtained during "idealized" conditions in a group of captive reindeer. Free ranging animals certainly are victims of inconviniant factors but observations in the field mainly supports our experimental data (pers obs.). High summer temperatures, leading to severe mosquito plagues together with disturbances from warble flies (Oedamega tarandi) and nose bot flies (Cephenomyia trompe) force the reindeer to seek refuge on higher ground during daylight.

A detailed knowledge of the activity patterns is not only of interest from a strictly theorethical point of view, but as Harcourt (1979) has pointed out, is also a useful tool for avoiding misleading information on the social structures and general behaviour of animals. It is of a direct practical value to be aware of the natural activity rhythm, especially in experimental and behavioural studies, since striking variations in the general performance of the animals are related to this.

Behaviour during the rutting season

The changing photoperiod regulates the reproductive processes by acting upon the hypothalamo-hyphophyseal system with a following release of sex hormones, which in turn are responsible for behavioural and physiological changes. Comparisons of androgen variations in some species of cervidae (Fig. 4) show that there are both similarities and differences.

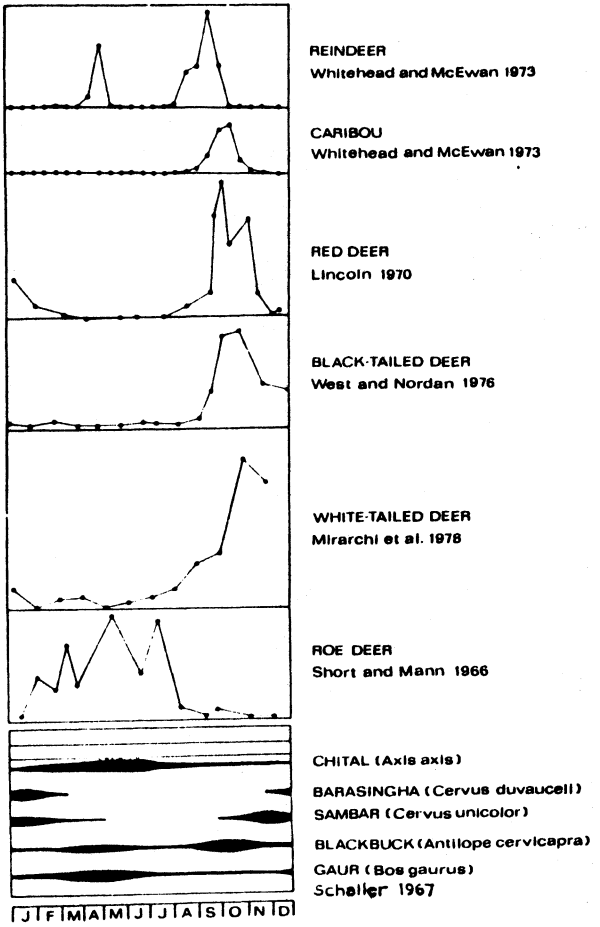

Figure 4.
Seasonal variations of androgen in some temparate-arctic cervidae species and rutting seasons for some ungulates on the Indian peninsula.

The common pattern is a more or less abrupt increase of the level followed by a somewhat gradual decline to a base level persisting until the next rut. Reindeer and caribou are considered to have compared to other Cervidae species comparable short rutting periods (Dauphiné & McClure 1974). The highest levels of androgen were found in the two studies of reindeer, in both cases exceeding 50 ng/ml blood. (III, Whitehead & McEwan 1973). A further peculiarity of reindeer is the occurrence of a second rut in March, not reported for other Cervidae (Whitehead & McEwan 1973, Meschaks & Nordquist 1962). This can be explained by the similarities in light-dark regimes in March and in September when the normal rut occurs. Since a declining daylength is also essential (Lincoln et al. 1977), the response of the reindeer is only partial. The timing of the rut is ultimately dependent on factors operating on the calving grounds limiting the brief period for optimum conditions for calf survival thereby selecting for a short and synchronized calving period. The timing of the birth period does not directly vary with latitude as is known to occur in different caribou populations in Canada but is to some extent dependent on local climatic conditions in the calving grounds.

Cervidae on the Indian peninsula (Fig. 3) do not posess such defined rutting periods and there are striking difference between groups of a species in different areas (Shaller 1967). The impact and necessity of an inherited photoperiodic control of reproductive activities in northern species is understandable from an ecological point of view, and the influence of climate seems to be of minor importance. In the tropical species it is

probable that the photoperiod plays a less important role in this respect. When northern Cervidae have been transported to other areas they have readily adapted to the new environments. The tropical species have failed to do so, and the main effect seems to be a more or less complete loss of reproductive cycles (Shaller 1967).

In addition to the influence of photoperiod, rutting activities are also influenced by the mutual stimulion between males and females. Reindeer herded in compact groups are sexually more active than those more loosely organized (Henshaw 1970). Furthermore mating seems to be more synchronized when females are simultaneously exposed to male courtship displays which includes both acoustic, visual and olfactory stimuli (Fraser 1968). This synchronizing effect by the males undoubtedly has survival value because the rut represents a period of extreme energy expenditure and it is not unusual for this to lead to the death of the bull (H. Larsson pers. comm). It would seem to be advantageous for the male to shorten this period, i.e. to initiating and synchronizing the ovulation of surrounding females, thereby increasing the possibility of successful mating with several females.

The photopeirod is far more reliable for timing the rutting period than e.g. climatic factors. The accuracy of the external watch is manifested in many ways as is described in (III). McEwan & Whitehead (1972) found that oestrous occurred 24 days after velvet was shed in reindeer and caribou. In the absence of pregnancy, subsequent oestrous occurred after 12 or 24 days. Conception in our reindeer was only observed

in 1977 (♀ H 28, ♀ C 30, and ♀ K 29 September). Comparing this with the dates when velvet was shed (Tab. 1) gives us $\bar{m}$ = 11.7 ± 1.2 days between the loss of velvet and oestrous.

	FEMALES			MALES		
Year/date	C	H	K	G	M	Q
1976	15/9	15/9	18/9	3/9	27/8	-
1977	20/9	15/9	18/9	1/9	26/8	31/8
1978	22/9	15/9	22/9	28/8	23/8	27/8

Table 1.
Dates for velvet shedding in adult reindeer.

This is in virtual agreement with McEwan & Whitehead's (1972) findings since his data indicates two cycles, one basic cycle of 13 days and another one of 24 days when ovulation has occurred without overt oestrous. Comparing the calving dates of our reindeer with those dates when velvet was shed shows that the short cycle of 12 days occurred in most cases.

In addition to the behaviours described in (II) the reindeer bull posesses three potential ways of chemical communication and pheromonal activity. The secretory activity of the preorbital gland increases during the rut; the prominent odor of the breath indicates a communicative vole; and the conspicuous odor in the urin makes an important contribution to the olfactory performance of the rutting bull.

While rutting behaviour and secretory activity of the preorbital gland develop slowly the appearance of odour in the urine and breath is very abrupt (III).

However, the chemical nature and origin of compounds responsible for these odours in not understood.

The breath odour can be compared with the "boar taint" of domestic swine (Patterson 1968). This compound, which is of steroid nature, is produced in the Leidig cells of the testes but has no androgen activity. It is contained in the submaxillary glands and is emitted through the saliva. It is possible that the reindeer taint could be derived from androgen as in the case of the domestic swine. But this possibility seems to be contradicted by the sudden appearance of the odour. If it was derived from androgen a more absolute correlation with the varying amount of the hormone could be expected. However, it should be noted that the abruptness of the appearances of the odour could be due to it being the treshhold value for detection by the human nose. Nevertheless the reindeer "taint" is taken by herders to mean that the bull is rutting. As in the boar the compound obviously circulates in the blood, deteriates the meat and imparts an unwholesome flavour.

During the actual rut the hairs on the corner of the lawer jaw are somewhat darker than otherwise, and this is appearantly caused by the strongly smelling saliva running from the mouth. That the odour is detected in the saliva does not mean that it is produced in or even mediated via the salivary glands. It may originate in the rumen tract. Prolonged periods of fasting in mammals causes the decomposition of stored fats and the production of large amounts of ketones, in humans mainly acetone. The period of fasting in our reindeer (III Fig. 6), corresponds fairly closely with the occurrence of the breath odour.

Conspicuously smelling urine has been reported from many ungulates during the rut, and it is a general observation that

urine has a basic role in the reproductive behaviour of mammals. Preliminary results show that the odour in the reindeer urine is due to a nitrogen compound occurring in very small quantities. Also, two ketones, 4-metyl heptanone and 2, 4-dimetyl heptanone which to us are almost odourless are secreted from the urine during the rut (Brundin 1978). The occurrence of these compounds in the preorbital but not in the interdigital gland indicates that these result from the action of androgen upon targetsorgans.

The sudden appearance of the urin odour is even more striking than the breath odor, and neither in this case is there any correlation between the odour and the amounts of androgen. The temporal appearance of the two discussed odours is noted in free-ranging reindeer (H Larsson pers comm), as well as in this study (III Fig. 6). Both odours are related to a considerable amount of androgen but if androgen is the primary cause it works by initiating rather than by directly influencing the processes resulting in the odours which can then be maintained by lower levels of androgen.

The underlying processes are far from understood, but the described circumstances indicate that they are somehow interrelated and emanate from the same physiological process.

In mammals a single odor may have different functions or result in different behavioural responses depending on the interpretation of the message by the reciever. Experimental supports are by no means decisive and the odours of the rutting bull may have several functions. An olfactory signal may show the status and mood to surrounding males but it might also act as an attractant to females. Self-marking with urine in

different ways is a common habit in ungulates (deVos 1967). The reindeer urin is spread to the frontal parts of the hindlegs during the tramping and urinating behaviour (Espmark 1964). Rubbing the hocks or urinating on the tarsal glands, as reported for caribou (Bergerud 1973), has not been observed in reindeer. During the rut the urine is more or less constantly distributed to the hindlegs and the bull itself becomes an olfactory signpost to conspecifics. The behaviour itself is associated with aggression and dominance and often terminates a sequence of aggressive acts. In this respect it would appear that the most likely function of the odor is to signal of dominance and threat.

It is difficult to single out specific roles for the breath odor other than those proposed above. In the domestic swine the boar breathes heavily into the face of the oestrus sow causing her to more readily assume a proper mating stance (Signoret 1970). Such deliberate behaviours have not been reported in other ungulates. The odour when it occurs is constantly emitted in the bull's breath and surrounding females are more or less always exposed to it.

Glandular structures and associated behaviour

The glandular elements in mammalian skin present a wide assortment of structures but can all be derived from two basic types, the holocrine and apocrine glands (Quay 1977). They occur in close association with hair follicles with orifices in or near the openings of the pilosebaceous duct. These components build up the extensive flora of specialized dermal skin glands (Shaffer 1940), which are of basic importance in mammalian olfactory

communication and in the production of pheromones. An outline of possible pathways for chemical communication is given in Fig. 5.

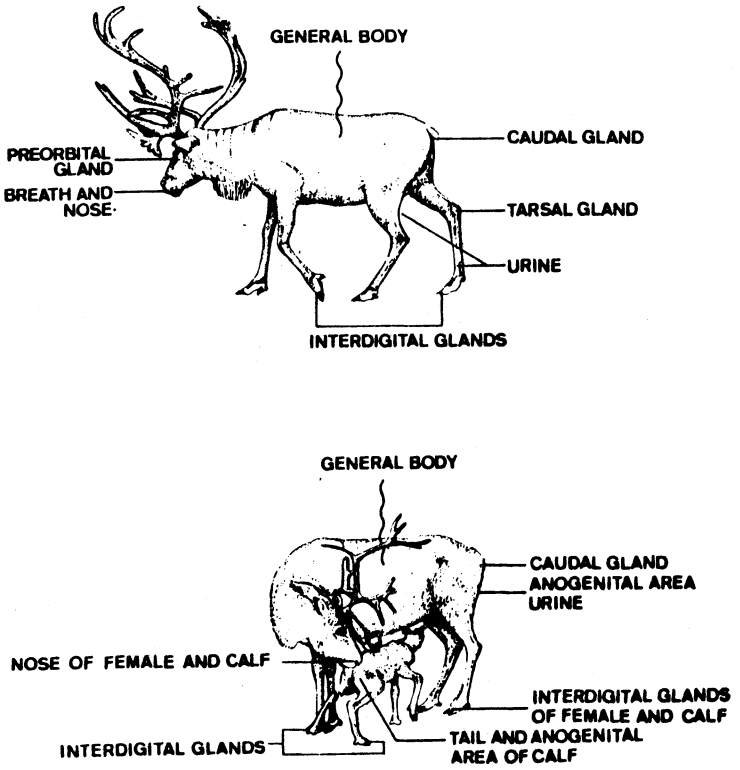

Figure 5
Sources for olfactory communication in reindeer. A summary of behavioural contexts and possible functions is given in II (Table 9) and below.

Studies on mammalian skin glands and olfactory communication have usually neglected the occurrence of scattered unspecialized skin glands. Their distribution in the reindeer is described in IV. Sweat glands in the general body area are primarily thermoregulatory (Montagna 1962). However, these holocrine and apocrine glands, produce a secretion, for a human nose best described as "typical reindeer". Both histologically and chemically those are less complex than those found in the specialized areas (Sokolov et al. 1977). The function of the fatty secretion is primarily as a water-repellent. The reindeer frequently sniffs its own general body surface and that of conspecifics (II Fig. 10 and Table 4), although the behavioural significance of this olfactory contact is not clearly understood. It should be stressed that the development and distribution of the apocrine glands can be subjected to a seasonal variation presemably inversely related to the development of fur. The apocrine glands (Cervus elaphus and Dama dama) and the holocrine glands (Capreolus capreolus) of the circumanal and circumgenital areas of females are to a varying extent enlarged during rutting season (Frankenberger 1956). A great difference in the activity of these glands in these species was found between sexually quiescent females and those on heat.

Female reindeer posess sudoriferous and sebaceous glands in the rump patch (IV). When approaching heat the anogenital area becomes darker and morphological changes of the area makes it easy to distinguishe a female in heat. Although no histological samples were taken from females in heat it seems likely

that the glands develop in a similar way to that found in other Cervidae. The frequency of sniffing and nuzzling of the anogenital area is also high at this time (II Fig. 9).

The reindeer belongs to the telemetacarpalian group of cervidae and posess tarsal, interdigital, preorbital and caudal glands. Detailed histological descriptions are presented by Quay (1955) and Müller-Schwarze (1977). Samples of these were collected from September to March in order to determine the amounts of sebaceous and sudoriferous epithelia (V). Quantitative differences presumable indicate changes in secretory activity and hence in behaviour. However, only the preorbital gland showed pronounced sexual and seasonal variations in activity, while the others were active all seasons. As a rule glands used in scent-marking are dominated by fat-producing sebaceous glands; an example being the subauricular gland in prong horn (Moy 1970). A well developed layer of apocrine tubuli indicates a capacity to produce more volatile substances. Apart from the preorbital gland which is mainly apocrine, the other glands are of the mixed type containing both holocrine and apocrine glands.

The interdigital gland is located in the dorsal interdigital skin. The most presumptive function for the interdigital secretion is surely that of laying tracks, though evidences are of a more indicative nature. However, the reindeer pay attention to interdigital secretion from conspecifics placed on the ground in a manner suggesting that it plays a role in the identification of social groups (Müller-Schwarze et al. 1978).

The secretion mainly consists of low-volatile fats and a long-term effect is suggested since the fats are decomposed to more volatile short aliphatic acids (Brundin et al. 1978). Numerous observations on free-ranging reindeer show that they do follow tracks. The identification of calves might be aided by these tracks (II) and it is to be noted that the interdigital gland is the only gland containing visible secretion on the hairs in newly born calves (pers. obs.). The scent tracks may be of several origins but the large sudoriferous glands in the ventral interdigital skin are probably important in this respect.

Pruitt (1960) describes how the frightened caribou rears up and tramps violently with his hindlegs, thereby depositing interdigital secretion on to the ground, leaving a strong smelling scent mark, that following conspecifics avoided.

A traditional view for the function of the interdigital gland is its role in greasing the antler tips while performing hindleg-head contact, (Espmark 1977). The antler growth-promoting function of hindleg-head contact is supported by observations that reindeer prevented from such contact grow deformed and assymmetric antlers. However, the main objection against this possible greasing effect is that the velvet itself contains large amounts of sebaceous glands, especially at the tips of the antler.

In order to trace the interdigital secretion 0.1 ml of a mixture of rhodanine and wool fat was injected into the bottom of the glandular pocket in March-May 1977 (unpubl. res). After

only a few hours the red colour was found on: the interdigital hair tuft and the hairs dorsally between the digits, on the nose due to licking, on the antler tips during hindleg-head contacts and on the hairs of the ventral parts of the fore feet. Traces were also found in tracks in clean snow. Thus secretion is distributed to several places of the body, and to the ground. The secretion seems to provide information about individuals or at least to indicate which sex is involved (Müller-Schwarze et al. 1978).

The tarsal gland gland located on the medial side of the ankle, shows a great individual variation in its gross appearance and in the development of the glandular layers (Mossing and Källquist in ms.). In the material examined here the variations are neither sexual nor seasonal but appear to relate to the individual. Such variation eventually led Quay (1955) to assume that the gland is a special female organ. Solokov et al. (1977) found that the tarsal secretion has greater chemical complexity compared with the secretion from the preorbital and interdigital glands. Our studies reveal that the tarsal gland is the least emphasized gland in reindeer and furthermore also paid little attention to in social interactions by conspecifics (II).

The caudal gland, (Müller-Schwarze et al. 1977), is located on the basal 2/3 of the dorsal part of the tail. It is the largest gland in reindeer and consists of both well developed sebaceous and sudoriferous glandular layers. The secretion is chemically complex but mainly consists of aldehydes and short aliphatic acids which provide a typical odour also apparent even in week-old calves.

The tail and anogenital area are frequently sniffed in two social contexts. First in maternal behaviour, when the mother sniffes the tail of her calf (Källquist and Mossing in ms). A similar sniffing of the tail occurs when a "strange" individuals enters a group (II). These two observations strongly suggest that the gland is essentially concerned with individual identification.

Another proposed function of the gland is its role in alarm situations (Lewin and Stelfox 1967). The alarmed reindeer assumes a typical position. The tail is raized which causes the rump patch to be more conspicuous.

Although the proposed alarm effect of odour remains to be established it may be concluded from available information on penned and free-ranging reindeer that the alarm response is mainly brought about by the visual display.

The depression in the skin anterior to the eye is a glandular area in many deer (Shaffer 1940). In reindeer the preorbital pocket is 1-2 cm deep and somewhat paler than the surrounding area. An immediate observation is that glandular activity is most pronounced in mature males during the rutting season (V). The apocrine part of the gland at this time is enlarged while the sebaceous part maintains the same activity throughout the year. The diverse development of apocrine epithelium in males, castrates and females strongly suggests a dependence of androgen.

The enlargement of the glandular epithelium makes the preorbital gland more conspicuous. Similar changes are reported in elk (Struhsaker 1967) and in Père Davids deer (Shaller 1978). Outside the rutting season no secretion is visible but during

the prerut and rut there are large amounts of fatty deposites on the rim of the pocket. The preponderance of sudoriferous epithelium indicates a capacity to produce air-borne substances. The main components of the volatile part consists of 4-heptanone and 2-methyl-4 heptanone (Andersson 1978).

The most obvious behavioural role is the widening of the pocket during agonistic encounters. It occurs in males and females and during all seasons, but is most frequent during the rut (III). The opening of the glandular pocket facilitates the emmittance of volatile compounds from the fundus of the gland where most of the apocrine epithelium is located. The behaviour itself is associated with dominance and aggression and odour is most likely a part of the threat.

The open glandular pocket creates a white area anterior to the red blood shot eye of the rutting bull, who emphasizes this by turning the side of his head towards the antagonist. This makes it likely that the pocket also is used as a visual sign.

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