THE ROLE OF THE TARSAL GLANDS IN THE OLFACTORY COMMUNICATION OF THE ONTARIO MOOSE - A PRELIMINARY REPORT.

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Abstract: From behavioral studies of moose and elk-hounds, the authors have concluded that the tarsal gland secretion (TGS) is the primary olfactory signal in searching out con-specifics. For this study TGS alcoholic extracts of 49 males and 49 females collected between October and December were analyzed by gas chromatography - mass spectroscopy. In 28 males (57%) and 17 females (34.7%) o-cresol was found as the major volatile component usually being accompanied by small amounts of higher homologs. The o-cresol content varied with sex, age and date from o-170% of the C_{16}-ethylester used as standard. Glands containing o-cresol were found in females of the same area and time period, while the males having these "active" glands were scattered in time and location. This led to the hypothesis that its presence could correlate with sexual activity in both genders. However, samples containing o-cresol did not elicit any sexual response from moose. This meant that no sexual pheromone was present in TGS. Our hypothesis is that o-cresol needs some synergetics and acts only as a conspicuous informer attracting the animal's attention and leading it to other more definitive olfactory cues which are being investigated. The study has shown that the correct answer to this problem will need investigation under simulated conditions in order to determine how the TG responds to sex hormone levels and to what degree its spectrum is contaminated by urine.

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The direct or indirect function of secretion of odoriferous substances is facilitation of communication (for review see: Müller-Schwarze and Mozell 1976). Depending on the location of the scent producing glands, or their absence in one gender or a sex-dimorphic spectrum of constituents (which can be influenced by physiological status or physical conditions), the produced odour can act as a primer, releaser, or informer (Müller-Schwarze 1976).

Generally speaking the olfactory signals are, for macrosmatic species, the most important communication system. They are independent of other sensory systems except taste (Schultze-Westrum 1970, Whitten 1969), but can reinforce or be reinforced by the visual, acoustic or tactile stimuli (Mykytowicz 1976), as long as one of these is not superior to them (Bubenik 1973).

The advantage of scents in comparison to other signals transmitted by the individual (except for anonymous visual marks left by animals, e.g. scrapes, fraying spots, etc.) is their relatively long lasting effect and the individuality of their own scent spectra, which enables self-advertising in absentia.

Existing knowledge of olfactory communication in moose is limited. According to Schaffer (1940), Haltenorth (1963), and Sokolov (1964), the well developed apocrine glands are antorbital. interdigital and tarsal. Metatarsal glands are not always present and no records exist about caudal or forehead glands, which are all well developed in cervidae (Bachnova and Bubenik 1958, Brownlee et al. 1969, Hofmann 1978, Lojda 1956, Müller-Schwarze et al. 1977, Volkman et al. 1978), or circum-anal or circum-vaginal glands as have been found in some other species (Frankenberger 1957).

Sweat and sebacous glands are distributed all over the moose body with density being dependent on body site and season (Sokolov 1964, Timmermann, pers. comm.).

We did not find any records, and we do not have any observations of our own on the use of antorbital secretion on signal trees by moose (Bubenik 1979), as occurs in red deer Cervus elaphus sp. (Darling 1936). Also, we did not find any reference to prepucial secretion in moose as it is the case in fallow deer, Dama dama (Kennaugh et al. 1977).

From observation of free ranging moose and the behaviour of elk-hounds when tracking moose (Bubenik 1976, 1979, Schultz 1931) it was without doubt that the tarsal gland (TG) scent is moose specific and has some social significance. The question was what its social role is and what are the most important constituents of tarsal gland secretion (TGS). This secretion, based on experience, has a very low evaporation rate and for humans is a very unpleasant, but easily perceived odour.

METHODS

Through the hunting seasons of 1976 and 1977 in the Thunder Bay Region of northwestern Ontario (October 11 to December 15), 98 TG pairs were collected and preserved in 250 ml of absolute ethanol of known residues, then stored in polypropylene bottles. It was conceivable that the TGS and/or its constituents could be influenced by sex, maturation, onset and duration of gonadal activity and rank (Bubenik, G. et al. 1977, Gordon and Bernstein 1973, Hager 1978, Holst 1969, Lee et al. 1976, Lincoln 1976, Lincoln and Guinness 1977, Lincoln et al. 1972, Katangole et

al. 1971, Müller-Schwarze 1967, 1969, Müller-Schwarze and Müller-Schwarze 1972). Therefore, when it was possible, we collected data which are indicators of these parameters, e.g. sex, age, date, hoof wear, behavioural and social circumstances.

After extraction of the TG with methylene chloride and its evaporation in a vacuum, the residue was analyzed in a Finigan 3200 gas chromatograph-mass spectrophotometer (GC and MS) with 3% OV 17 columns supelcoport 60-80 within 50 to 300^{o}C. In order to be sure that very volatile constituents were not lost by evaporation of methylene chloride, the controls were only blown down.

Both bull (Geist 1966, McMillan 1954) and cow moose (Hristienko, pers. comm.) urinate on their tarsi, as do many other Odocoileinae. Urine samples from a captive bull were analyzed by GC-MS. TGS specificity was checked by GC and MS analyses of skin samples from the bell, shoulder and belly, where dense areas of sweat and sebaceous glands occur.

In order to quantify the secretory activity of some of the highly odiferous constituents, their peaks were measured and expressed as percentages of the permanently present compound, the ethyl-ester of palmitic acid (C_{16}-EE-standard). We tested the releasing effect of crude extract, single and identified constituents, or their combinations (due to possible synergistic effects noticed by Müller-Schwarze and Müller-Schwarze 1971, Müller-Schwarze 1974a) as well as the neutral, basic and acidic fractions of TGS in compositions close to that shown in the GCs spectra. The test animals were penned moose (two 1½ year old bulls, one 2½ year old and one 3½ year old cow) and an experienced Norwegian Elk-hound. For this purpose, strips of filter paper carrying 3 droplets of different concentrations of odour were offered in a "cafeteria-style" test, or were directly brought before the nostrils.

In the study of TG from hunted moose we did not have a complete collection of corresponding ovaries and testicles, or blood samples in order to follow the gonadal activity in relation to TGS. In a few specimens we obtained the front hooves and checked their wear (Bubenik et al. 1979) in order to see if different rates of mobility would correlate with TGS activity.

Assuming that TGS is activated by sex-hormones, an unworn hoof and moderate TG secretion should indicate the start of sexual arousal. High wear and high TGS should occur in sexually long active moose, and low TGS combined with high hoof wear should indicate declining sexual activity. No wear with no TGS was expected in moose before or past estrous.

Based on our observations on behaviour of moose bulls and cows in different phases of the sexual cycle (Bubenik 1979, Thompson 1949) which was similar to that in red deer (Lincoln and Guinness 1973, 1977, Bubenik unpubl. observ.), we conclude that the TGS could be influenced by sex hormone levels in particular.

In order to avoid possible biasses in evaluation of TGS activity (TGSA), we constructed a hypothetical curve of TGSA in relation to development of estrous (Fig. 1). This was based on the assumption that TGS in the anestrous cow could disappear very fast, to avoid searching and courting by bulls. From our observations, we expected that the TGs need about 2½ days to be maximally activated. In cows it should remain in this performance

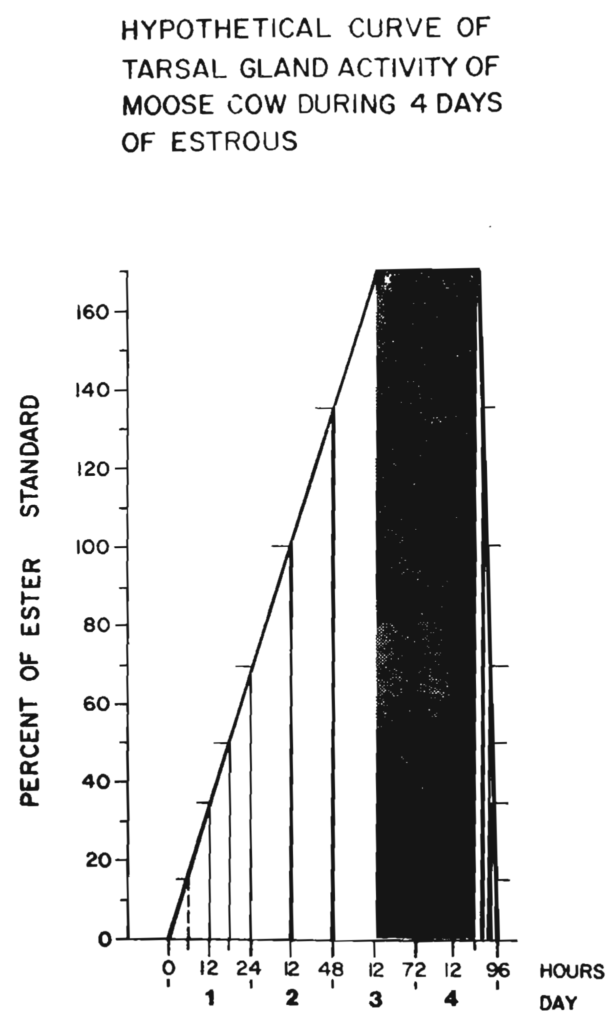


FIGURE 1

at most for another 24 hours, depending on the fate of the mature ovum. Considering the behaviour of a cow in estrous towards the bull, we concluded that whether she conceives or not, the TGS could drop to zero level within 6 hours, at any time in this 3½ day period.

For bulls, we did not attempt to construct a similar curve of TGS-activity since the onset and duration of testosterone secretion in ungulate males is dependent on at least three factors: the maturation status, pheromonal stiumlation, and social rank (Bamberg and Bubenik in prep., Bubenik, G. et al. 1977, Dessi-Fulgheri et al 1976, Hager 1978, Holst 1969, Katongole et al. 1971, Kram et al. 1969, Lincoln et al. 1972, Müller-Schwarze 1974b, Mykytowycz 1976, Mykytowycz and Dudzinski 1966, Mykytowycz and Fullagar 1973, Pinsker 1978, Rose et al. 1972, Signoret 1976). If such a curve could be drawn we would expect more than one peak and different heights of these, and the course of the curve would be individually highly variable. Our records of where the moose were shot offered the opportunity to check if the TGS in cows is synchronized geographically. Assuming that the odoriferous secretion of the TG is under control of sex-hormones, a positive finding could be used as indirect proof for hormonal control of TGS, and synchronized estrous in moose cows as suggested by Markgren (1964), and for black-tailed deer (Odocoileus hemionus columbianus), by Thomas and Cowan (1975), red deer by Lincoln and Guiness (1977), caribou (Rangifer caribou) by Bergerud (1975) and chamois (Rupicapra rupicapra) by Meile and Bubenik (in prep.) and is known in other ruminants (Fraser 1968, Grau 1976, Mykytowycz 1976, Sambraus and Waring 1975, Wilson 1968).

Both genders in moose urinate on the tarsi, so it is possible that odoriferous constituents in urine could remain on the TG we collected. To check for the presence of compounds similar to those in TG, we analysed urine from pitholes in September, and urine of a 1½ year old bull in February, whose rut was induced by i.m. applications of 275 mg. of testosterone cypionate (69 mg/100 kg live weight). Urine samples for this purpose were taken before and after the peak of sexual arousal.

In order to decide if TGS acts as an informer or releaser (Müller-Schwarze 1976), we chose flehmen as the most reliable indicator of sexual interest by bulls (Bubenik 1979, Lott 1974, Sambraus and Waring 1975).

RESULTS

From the high number of constituents representing 44 fractions, the following were later positively identified: ortho-cresol (OC), which gives the unpleasant and long lasting odour to the TGS; small amounts of para-cresol (PC) and different phenols in some glands; and in just a few TG an unidentified lactone was also present.

In all extracts the palmitic acid ethyl-ester (C_{16}-EE) was the permanent constituent, and we used its peak as the standard for the OC level.

Urine collected from pits did not contain phenols or its homologs, but urine collected under the influence of a testosterone implant was rich in PC and OC on day 1 and day 7 respectively (Table 1). It is worthwhile to mention that similar changes in cresol (para and meta) were found in the temporal glands of elephants (Adams et al. 1978, as compared with Wheeler, pers. comm.).

Table 1. Analyses for cresol in urine from a bull moose under testosterone booster.

Day from Injection	P-Cresol	O-Cresol
0	nil	nil
1	high	nil
2	nil	nil
3	nil	nil
*		
7	nil	high
8	nil	nil

* Days 4,5,6 urine samples unobtainable due to the bull's behaviour.

THE BIOTESTS

As it is shown in Table 2, the responses of moose and elk-hound to the constituents were not quite similar and also varied with sex in the moose. How far this diversity was dependent on physiological state, behavioural mood, weather and of course on synergetic effects of the constituents, is open to question.

Table 2. Example of results of "cafeteria-style" bioassay.

Compound	Moose	Moose	Elk-hound
Ortho-cresol pure	1	1	1
Meta-cresol pure	1	1	1
Para-cresol pure	2	2	0
Phenolic-Carbolic Acid	1	1	1
Moose Acidic, Non-Phenolic Extract	3^a	1	1
Moose Basic Extract	1	1	1
Moose Phenolic Extract	4	3^a	3^b
Moose Neutral Extract	2	2	1

Code: 0 = repugnant

1 = no interest

2 = reaching to sniff sample, attention span < 15 seconds

3^a= in moose as in 2, with attention span > 15 seconds, will follow a few feet if sample moved

3^b= in Elk-hound

4 = as in 3^a plus licking air next to sample and attempt to lick and ingest sample

The general impression of these tests was as follows: for moose and elk-hound the crude phenolic extract was equally attractive, pure PC was repugnant for the elk-hound, and slightly less for moose. No response was given for OC, PC and MC, phenolic acid or basic extract.

Non-phenolic extract was attractive only for bulls, and both genders were slightly interested in the neutral fraction.

That cresols were repugnant for elk-hound and moose was surprising, and speaks for the assumption that its effect is dependent on the presence of synergistically acting constituents.

In this study we were unable to prove if OC extracted from our samples originated only from the TG or at least partly from urine splashed over the heels. Until this question is definitively solved, we will consider the OC-fraction as the important constituent of TGS. We have also to stress that no highly volatile compounds have been found in the TGS extracts.

The skin probes from the different parts of the body did not contain any traces of phenols or phenolic homologs.

INTENSITY OF TGS ACTIVITY

The OC-peak levels, expressed in percentage of C_{16}-EE Standard were quite variable, with values between zero and 170 (Fig. 2). Due to the fact that we cannot find references concerning the seasonal activity of TG in moose and/or its dependence on the sexual cycle and maturation status, we evaluated separately the maturation classes of both genders in two different ways.

Using the same degrees of OC-levels as established in Fig. 1 (hypothetical curve of TG activation during the female's estrous) we searched for the frequency of distribution in both sexes (Fig. 3). From this graph it is evident that the most active moose were the older

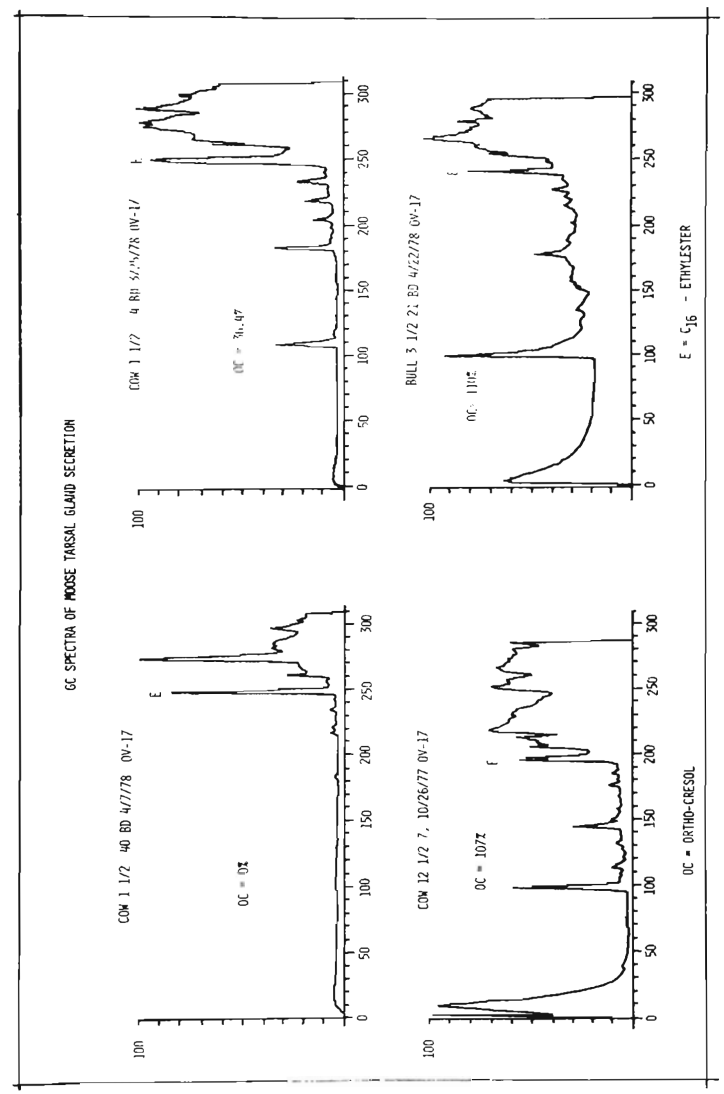


FIGURE 2

teen bulls, e.g. 2 and 3 years old and then cows older than 2 years, followed by yearling cows, and prime bulls. Much lower TGS was found in yearling cows and very low in yearling bulls. The lowest values were in prime bulls. Although the sample size is small, the calves as a class, had the largest percentage of tarsals with no o-cresol. The lowest number producing no OC was in the older teens, which might indicate that in October to December this class was the most sexually active.

The percentage of cows with zero OC-level was 33% for yearlings, 46% for older teens, and 42% for primes. The most active class in which OC-levels correspond to all possible classes of a 4 day estrous, were older teens, followed by prime cows. The yearling cows might also be very active, having a much wider pattern of TG activity, but none were found close to or over 100% of the standard.

Figures 4 to 7 show four maturation classes of bulls and cows according to the OC-levels, date of death, and in a few specimens, the hoof wear rate.

Figures 4A and 6A for calves show generally zero and in a few specimens very low TGS. Hoof wear, if known, was minimal.

The TGS in yearlings, Figs. 4B and 6B, was probably rising during October in both genders and declining during November. Due to an insufficient number of specimens it is impossible to know if the one zero in females and one nearly 50% activity in males are representative for this class in December.

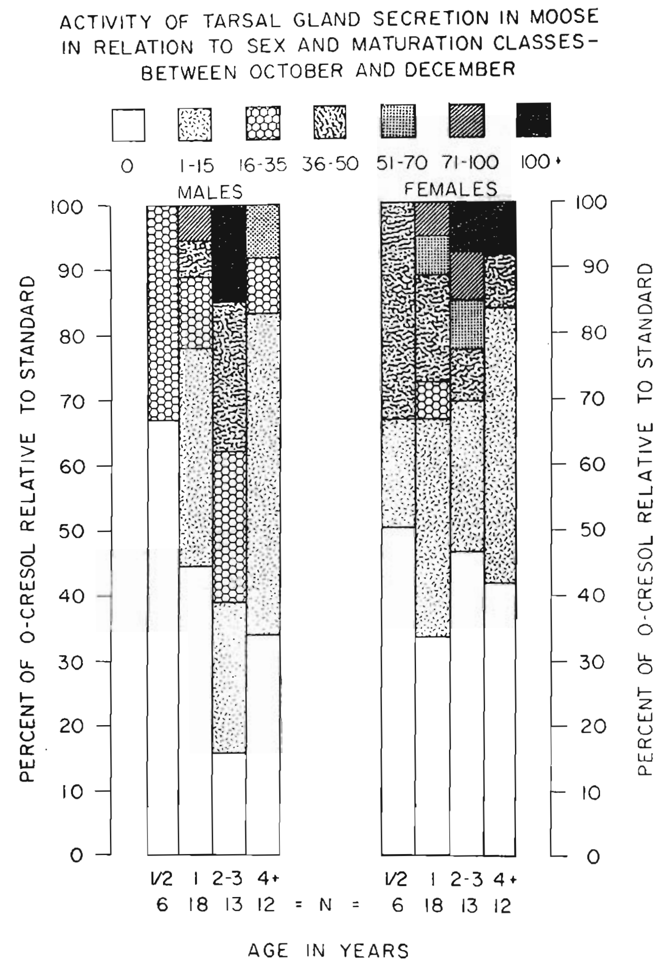
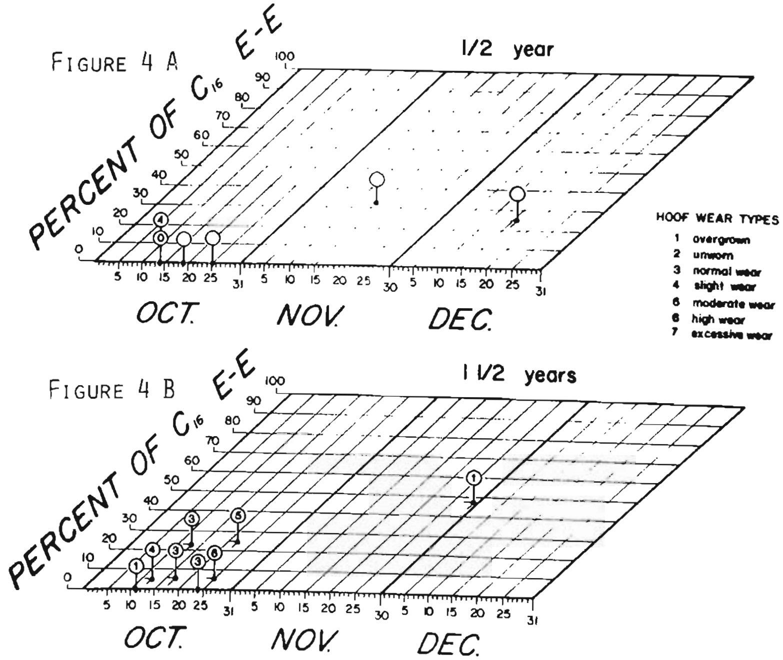


FIGURE 3

♂ MOOSE TARSAL GLAND ACTIVITY IN % OF STANDARD

FIGURE 4 A

FIGURE 4 B



Figures 5A and 7A show the TGS activity of older teens. In bulls there is a trend to raise the TGS from October to November, but the secretion is relatively low, e.g. slightly over 40%. In contrast, the cows show a different picture. Under the assumption that the TGS is related to estrous and can last only a few days, we suggest that there were three peaks

with different levels of secretory activity. The first peak around October 12, with a relatively low level; the second peak about 14 days later, around October 25, with one specimen having OC level of 122% of standard; and finally the third peak which is around November 15. Unfortunately no cows of this class were killed in December.

The TGS in prime bulls (Fig. 5B) and cows (Fig. 7B) was the most interesting. The bulls' TGS was generally extremely low, between 1 and 25%, with one specimen from October 15 at 52% of the standard.

If our hypothesis on activation of the TGS sex hormones is true, then cows killed in October were in anestrous and a few repeated the estrous in mid-November and mid-December. Unfortunately there were not too many moose in our collection in which the TG and hoof were both available, so the hypothesis remains unproven for now.

Finally we tested graphically if in the same geographical areas a synchronization of TGS occurs. The data plotted in Fig. 8 seems to support this idea and points out that in October (e.g. one month after the first estrous period with the most pronounced rutting activity) at least one other, but perhaps two new peaks of activated TGS were detected, and in November and December one estrous period has occurred.

♂ MOOSE TARSAL GLAND ACTIVITY IN % OF STANDARD

FIGURE 5 A

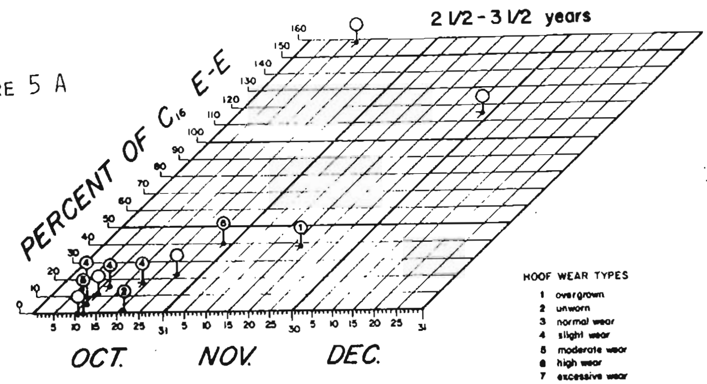
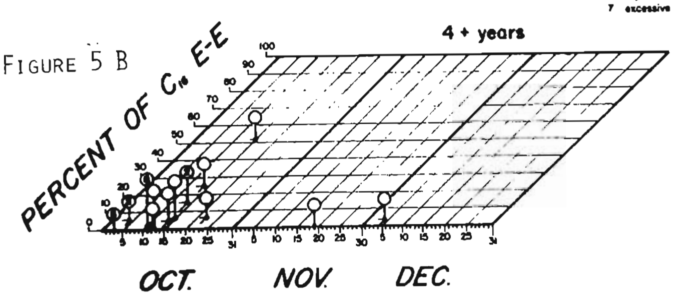


FIGURE 5 B



* No number in circle means hoof wear estimation unavailable

♀ MOOSE TARSAL GLAND ACTIVITY IN % OF STANDARD

FIGURE 6 A

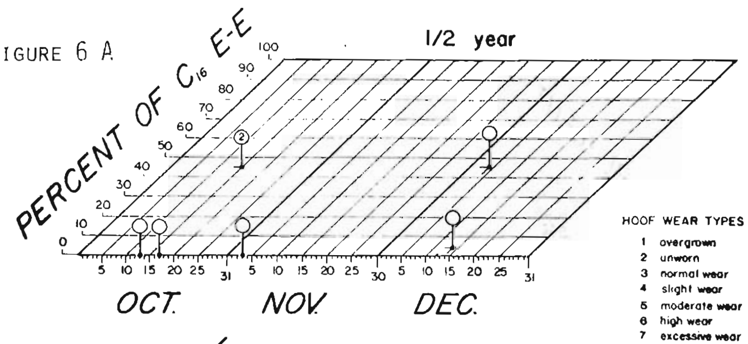
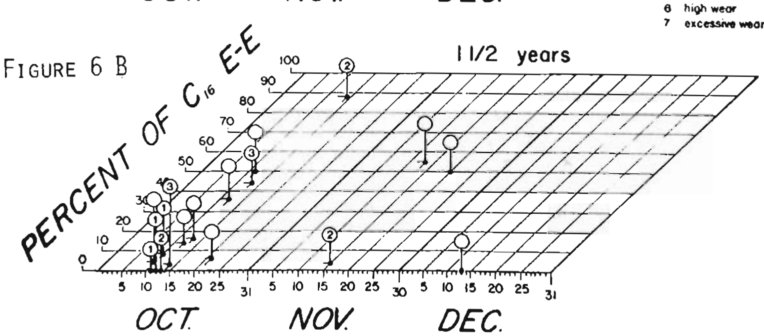


FIGURE 6 B



♀ MOOSE TARSAL GLAND ACTIVITY IN % OF STANDARD

FIGURE 7 A

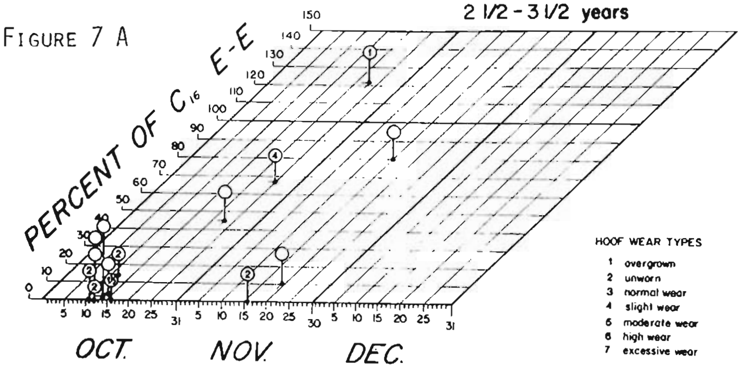
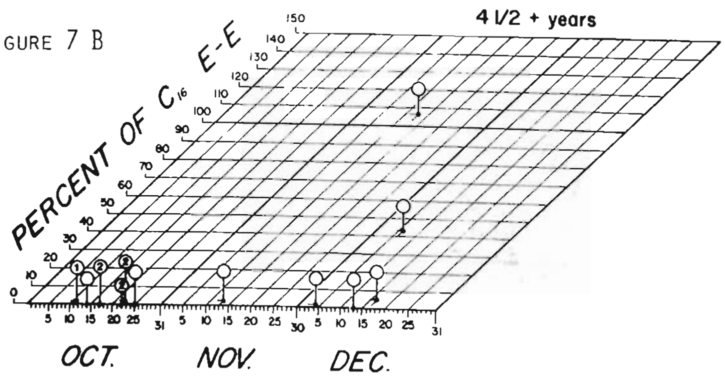


FIGURE 7 B



HYPOTHETICAL ESTRUS PERIODICITY IN MOOSE COWS IN DIFFERENT AREAS OF THUNDER BAY REGION AS EXPRESSED BY INTENSITY OF TARSAL GLAND SECRETIONS - BETWEEN OCTOBER 11 AND DECEMBER 15

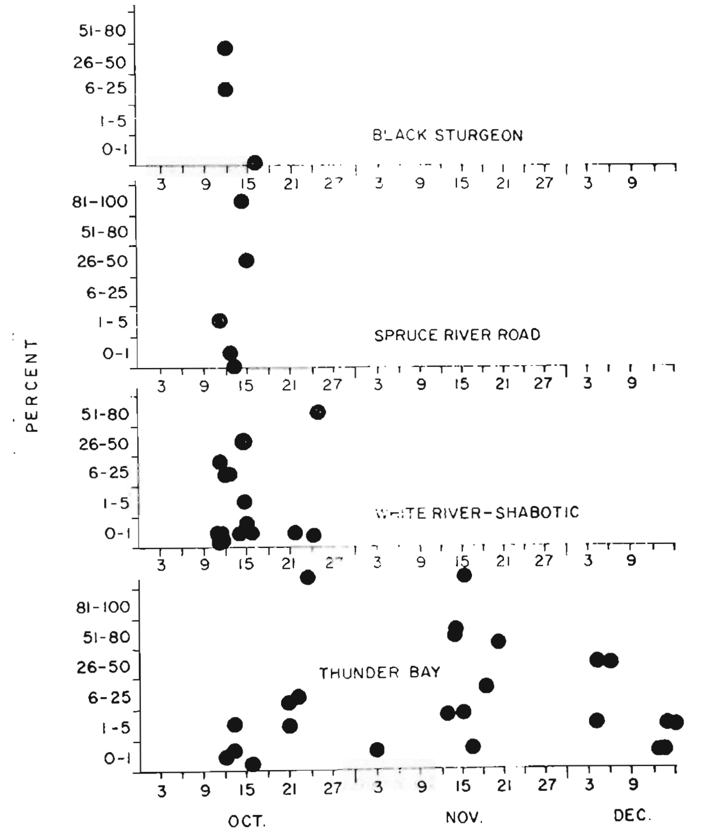


FIGURE 8

CONCLUSION

The TGS of moose from October to December is genus specific among telemetacarpal cervids as compared with the observations of Müller-Schwarze (1969, 1974a, 1976), and Volkman et al. (1978). Presently we do not know if, or how much, the TGS is contaminated by OC originating from the urine. Also, how fast can the OC be washed away by urine not containing OC or by walking in water? In this regard, we could be incorrect to suggest that the most odoriferous constituent of moose TGS is ortho-cresol. Support for the suggestion that the TG secretes OC and other phenols is in the finding that OC or PC was not always present in the male's urine. Also, none of the single constituents, different extracts, or crude scent elicited flehmen, e.g. presence of pheromones, as does the urine of moose in estrous. However, it is highly probable that the OC effect is dependent on other synergetics. We ascribe to this compound the role of an "alerting informer", e.g. of a long lasting, very strong scent, which elicits interest and possibly the olfactory checking of the track, where sooner or later other information with releasing or priming effects would be found. This, we suggest, happens when pitholes and urination spots are left (Bubenik 1979). We do not consider OC and accompanying homologs as sex pheromones with priming or releasing effect, because in no tests did moose bulls respond to the TGS by flehmen.

The great diversity of OC-levels in both genders, and the pronounced sex-dimorphic pattern and time variation of TGS activations (Figs. 4 to 8) lead to the hypothesis that tarsal gland secretion of OC is dependent on sex hormone levels. If the female has the ability to

destroy the cresols within hours, this hypothesis helps to explain why the OC-secretion has a limited duration in females and is long lasting in males.

The variation of OC maxima and minima in different maturation classes could also be sex hormone dependent, if we consider that the onset and end of testosterone secretion, and its levels as well, are dependent on the maturation status of the individual (Bubenik, G. et al. 1977, Lee et al. 1976, Mykytowicz and Dudzinski, 1966, Mykytowicz and Fullagar 1973, Wilson 1968).

Since TG from September were not represented in our collection, it was not surprising for us that TGs of prime bulls from October onward had zero or very low OC values. This was expected since, in this class, the hoof had begun to, or was already regenerated (Bubenik et al. 1977). Bulls of the senior class were out of the rut and did not have the darker head pigmentation, which we relate to the level of circulating testosterone (Bubenik et al. 1977, Bubenik et al. in prep.).

It might appear striking that among the teen bulls (Fig. 5A), whose OC secretion in TG was most active, some of them have had very low or zero OC values. This finding must not be surprising if social inferiority in moose bulls can influence the testicular activity in a similar way as it has been found recently in red deer plasma (Bamberg et al. in prep.), white-tailed deer (Bubenik, G. et al. 1977), and was observed and histologically determined in a red deer population (Lincoln and Guiness, 1977; Pinsker 1978), chamois (Hager 1978) and in many other species as well (Holst 1969, Gordon and Bernstein 1973, Rose et al. 1972).

If the hypothesis concerning activation of OC secretion by sex-hormones is correct, then we have to conclude that most of the later matings rely on the older teen bulls on the one hand, and on the other, that an important percentage of cows cannot conceive in September and experience two or more estruses before getting pregnant during November and December.

Should the hypothesis be verified that OC in TGS is dependent on sex hormone secretion in both genders of moose and that OC is an alerting informer of this physiological status, then it could be a very important tool in moose management.

The OC odour of TG can be easily detected qualitatively and to a certain degree it could be quantified. The OC values of TGS could be estimated by an experienced checker and together with hoof wear, this would be a very simple method to gain insight into the sexual cycles of both genders. It would allow estimation of performance of bulls during winter, length of calving period and reproduction success (e.g. cow/calf ratio before the fall), and last but not least, impact upon the demographic structure and population behaviour (Bubenik et al. 1975).

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