

## Scent marking by Alaskan moose: characteristics and spatial distribution of rubbed trees

R. TERRY BOWYER

*Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775-7000, U.S.A.*

VICTOR VAN BALLEMBERGHE

*Pacific Northwest Research Station, U.S. Forest Service, 3301 C Street, Suite 200, Anchorage, AK 99503, U.S.A.*

AND

KAREN R. ROCK

*Institute of Arctic Biology, University of Alaska, Fairbanks, AK 99775-7000, U.S.A.*

Received May 30, 1994

Accepted August 30, 1994

BOWYER, R.T., VAN BALLEMBERGHE, V., and ROCK, K.R. 1994. Scent marking by Alaskan moose: characteristics and spatial distribution of rubbed trees. *Can. J. Zool.* 72: 2186–2192.

We studied scent marking (rubbing of trees) in Alaskan moose (*Alces alces gigas*) in interior Alaska during 1989. Pole-sized trees were stripped of bark and rubbed by adult female and adult male moose; marking by females occurred during the peak of rut (late September – early October) when most females were in estrus, whereas marking by males was in late rut (mid-October – November). Moose selected white spruce (*Picea glauca*) as well as trees with particular physical characteristics for marking. The tops of 18.5% of 54 trees marked by moose were dead, whereas only 0.5% of 201 trees available for marking had dead tops. The distribution of scent-marked trees on rutting grounds was not spatially clumped. We hypothesize that rubbing of trees by females advertises their estrus, and that rubbing by males late in rut serves to attract females not successfully bred early in rut and may help prime estrus in these females.

BOWYER, R.T., VAN BALLEMBERGHE, V., et ROCK, K.R. 1994. Scent marking by Alaskan moose: characteristics and spatial distribution of rubbed trees. *Can. J. Zool.* 72 : 2186–2192.

Nous avons étudié le marquage d'odeurs (frottements sur les arbres) chez l'Original d'Alaska (*Alces alces gigas*) à l'intérieur des terres en Alaska, en 1989. Les grands arbres étaient dépouillés de leur écorce et frottés par les femelles et les mâles adultes; le marquage des femelles se produisait au plus fort du rut (fin de septembre – début d'octobre), au moment où la plupart des femelles étaient en chaleur, alors que le marquage des mâles se faisait surtout à la fin du rut (mi-octobre – novembre). Les originaux choisissaient surtout des Pins blancs (*Picea glauca*) et repéraient les arbres à caractéristiques particulières. La cime de 18,5% des 54 arbres marqués était morte, alors que parmi les 201 arbres disponibles, seulement 0,5% avaient la cime morte. La répartition des arbres marqués n'était pas contagieuse. Nous croyons que les femelles marquent les arbres pour signaler qu'elles sont en chaleur et que le marquage des mâles à la fin du rut sert à attirer les femelles qui ne se sont pas reproduites au début du rut et peut déclencher l'oestrus chez ces femelles.

[Traduit par la Rédaction]

### Introduction

The role of scent marking in mammalian communication has received considerable attention (Bossert and Wilson 1963; Gleason and Reynierse 1969; Eisenberg and Kleiman 1972; Johnson 1973; Thiessen and Rice 1976; Peters 1980; Müller-Schwarze 1983; Gosling 1985). Scent marking typically involves the deposition of a pheromone intended to elicit a response from a conspecific; a visual component is often added to make such marks more obvious (Ewer 1968). Scent-marking behaviors of many ungulates have already been described (for reviews see Coblenz 1976; Gosling 1985), and there is extensive information on the glands involved and pheromones released during these behaviors (Quay 1959; Quay and Müller-Schwarze 1970; Müller-Schwarze 1971; Kennaugh et al. 1977; Müller-Schwarze et al. 1978a, 1978b; Volkman et al. 1978; Atkeson and Marchinton 1982; Flood et al. 1989; Odend'hal et al. 1992). Indeed, North American cervids exhibit an especially complex array of scent-marking behaviors (Geist 1966; de Vos et al. 1967), and numerous authors have contributed to our knowledge concerning the functions of these intricate patterns (de Vos 1967; McCullough 1969; Müller-Schwarze 1972; Moore and Marchinton 1974; Kile and Marchinton 1977; Wemmer and Murtaugh 1980; Nielsen et al. 1982;

Marchinton and Hirth 1984; Bowyer 1986; Bowyer and Kitchen 1987; Miller et al. 1987; Benner and Bowyer 1988; Marchinton et al. 1990; Miquelle 1991). A complete synthesis of scent marking among North American cervids, however, requires additional data for some species.

For moose (*Alces alces*), descriptions of rutting pits and behaviors associated with this activity have been documented previously (Tanton 1920; Thompson 1949; Woodin 1956; Geist 1963; Lent 1974), but only one study has adequately addressed the function of this behavior (Miquelle 1991). This lack of extensive data is not surprising because moose often inhabit dense boreal forests (Peterson 1955), making detailed observations of their behavior under natural conditions especially difficult.

Scent marking of trees (sign-posting or rubbing) by cervids is likewise well documented (for reviews see Bowyer and Kitchen 1987; Benner and Bowyer 1988) but such behavior is poorly known and unstudied in moose. Our purpose was to describe the scent marking of trees by Alaskan moose (*A. a. gigas*), to test whether moose exhibited preferences for particular species of trees to mark, and whether the distribution of marked trees on rutting grounds was random. We also propose a new hypothesis for the function of this behavior.

## Methods

### Study area

We conducted this study in the eastern 150 km<sup>2</sup> of Denali National Park and Preserve in interior Alaska, U.S.A. (63°45'N, 150°W). Moose typically occur at elevations of 750–1200 m in a broad valley bounded to the north by rugged foothills and to the south by steep mountains of the Alaska Range. Dominant trees and shrubs include white spruce (*Picea glauca*), black spruce (*Picea mariana*), resin birch (*Betula glandulosa*), and several species of willows (mostly *Salix pulchura planifolia* and *S. glauca* in areas where we sampled) (Miquelle et al. 1992).

Moose in the east end of the park rut in traditional areas (rutting grounds), that are characterized by open stands of spruce, often located near the tree line, with willow understories (Van Ballenberghe 1992). About 150 moose occurred on our study area, with densities on rutting grounds ranging between 0.7 and 1.8 moose/km<sup>2</sup> (Molvar et al. 1993).

### Sampling procedures

Aerial photographs of segments of two rutting grounds where we observed moose scent marking, encompassing approximately 7 km<sup>2</sup> each and located about 5.5 km apart, were gridded and Cartesian coordinates were selected randomly. At each of these 20 random points we established a 50 × 50 m plot, which was searched systematically by at least three people for trees scent marked by moose. Such trees were easy to identify and locate because moose had stripped away side branches from the tree and removed the bark from the trunk. We determined an adequate number of plots by examining reduction of variation in the number of scent-marked trees per plot as sample size increased (Kershaw 1964). Because we sampled plots prior to rut in September 1989, our sample undoubtedly included trees that had been scent marked by moose over several years. Also, we were not able to differentiate between trees scent marked by male and female moose. We determined the availability of trees for scent mark by nesting a 10 × 10 m plot randomly in one corner of our larger plot and examining all trees in that plot.

For each tree sampled we recorded the diameter of the tree at breast height (dbh), measured at 137 cm above the ground, the height of the first branch above the substrate, measured along the trunk of the tree, whether the tree was dead or had a dead top, and whether the bark was smooth or rough (rugose or scaly). For trees that were scent marked by moose, we also recorded the height of the midpoint of the scent mark (the area with bark removed) above the substrate, the diameter of the trunk at the midpoint of the scent mark, the distance between unbroken branches encompassing the mark, and the length of the mark. All measurements were made to the nearest 0.1 cm.

Differences between the characteristics of trees that were scent marked by moose and those that were not were made with a *t* test or two-sample *Z* test for proportions (Remington and Schork 1970); *P* values from those tests were adjusted with a sequential Bonferroni correction for multiple comparisons (Rice 1989). We investigated the degree to which trees were clumped by using the variance:mean ratio; a random distribution has a ratio equal to unity, whereas a value < 1 implies a regular distribution and a value > 1 suggests clumping (Whitaker 1975). We determined whether such clumping of scent-marked trees was random (i.e., departed a Poisson distribution) with a  $\chi^2$  test, and pooled cells ( $\geq 6$  trees) to meet the assumptions of this procedure (Whitaker 1975).

## Results

Moose typically initiated the scent marking (rubbing) of small trees and large shrubs by smelling the trunk about 1 m above the ground. Females bit off side branches and males broke them off with their antlers. Bark was then stripped from the tree using either the incisors or, for most males, the antlers (Fig. 1). The area with the bark stripped away was smelled

and occasionally licked; the forehead, sides of the face including the preorbital gland, and often an area behind the ears were rubbed on this area. Bark stripping and rubbing of the head on the tree were often alternated during scent marking. Both dominant males and females behaved aggressively toward other moose that approached scent-marked trees, and if the initial moose was displaced by aggressive behavior, the dominant animal also scent marked the tree. Females were attracted to trees marked by males, and several would often gather around such a tree, sometimes rubbing the scraped tree. Social interactions around rubbed trees were generally short in duration (< 1 h). We detected a musky smell on trees after they were scent marked by moose, but the smell was not strong and was somewhat masked by the odor of the exposed meristem, which was especially strong in white spruce. Females scent marked trees most often near the peak of rut in late September and early October (when most were in estrus), whereas males tended to mark trees in mid-October to November following the first estrus in females.

Moose selected trees to scent mark on the basis of their physical properties (Table 1), as well as the species of tree (Fig. 2). White spruce were scent marked more often than they were available on rutting areas, whereas willows (mostly *S. glauca*), black spruce, and resin birch were marked less than expected from their availability in the environment (Fig. 2). The same pattern was evident even when we eliminated trees > 22 cm dbh (Fig. 2, inset), which moose did not scent mark (Table 1).

Typically, trees scent marked by moose were pole-sized spruce with smooth bark, which had the branches removed and the bark stripped from the tree (Table 1). Trees scent marked by moose often had tops that were dead, presumably as a result of marking behavior (Table 1). This was particularly evident for scent-marked white spruce; of 34 of these trees, 23.5% had dead tops, whereas of 108 unmarked white spruce, only 0.9% had dead tops ( $Z = 8.50$ ,  $P < 0.001$ ). When the same comparisons were made for willows and black spruce, the differences were not significant ( $P > 0.10$ ).

The number of scent-marked trees in 20 plots, each of 2500 m<sup>2</sup>, was  $2.7 \pm 2.03$  (mean  $\pm$  SD). The variance:mean ratio (1.5:1) suggests that these trees were slightly clumped, but this pattern did not differ significantly from a Poisson distribution (Fig. 3). When white spruce were considered alone, we obtained a similar result; the number of scent-marked trees per plot was  $1.7 \pm 1.49$ , and the variance:mean ratio was 1.3:1. Similarly, this pattern did not differ from a Poisson distribution ( $\chi^2 = 2.14$ , 2 df,  $P > 0.50$ ). Unmarked trees on plots (100 m<sup>2</sup>), however, were highly clumped (variance:mean ratio 7.6:1) as were unmarked white spruce (variance:mean ratio 2.9:1).

Of 108 unmarked white spruce, 53% had smooth bark, yet 85% of 33 scent-marked white spruce had smooth bark; this difference was highly significant ( $Z = 4.07$ ,  $P < 0.001$ ). Conversely, 100% of 60 unmarked willows were smooth-barked, whereas 8% of 14 scent-marked willows possessed this characteristic, again a highly significant outcome ( $Z = 5.40$ ,  $P < 0.0001$ ). Only 3% of 29 unmarked black spruce had smooth bark, but 29% of 7 marked black spruce had smooth bark; this difference was not significant ( $Z = 1.49$ ,  $P > 0.13$ ).

The mean dbh of scent-marked white spruce was 5.6 cm, but for unmarked white spruce was 17.8 cm. Willows scent



FIG. 1. Adult female (left) and adult male (right) Alaskan moose scent marking a white spruce by stripping the bark and rubbing parts of the head, interior Alaska, U.S.A. Photographs by V. Van Ballenberghe.

TABLE 1. Physical characteristics of trees scent marked or not scent marked by Alaskan moose on rutting areas in Denali National Park and Preserve, Alaska, 1989

	Marked					Not marked			
	$\bar{x}$	SD	Range	<i>N</i>		$\bar{x}$	SD	Range	<i>N</i>
Height of first branch above the substrate (cm) <sup>a</sup>	50.7	29.0	10–165	49	*	70.9	48.6	5.0–253.0	194
Diameter at breast height (cm) <sup>a</sup>	6.9	5.3	0–22	54	ns	8.4	11.5	0.0–57.3	202
Dead (%) <sup>b</sup>	13.0	—	—	54	ns	4.5	—	—	202
Top of tree dead (%) <sup>b</sup>	18.5	—	—	54	*	0.5	—	—	202
Bark smooth (%) <sup>b</sup>	79.6	—	—	54	*	60.7	—	—	202

NOTE: \*, significant at  $P = 0.05$  following sequential Bonferroni correction; ns, not significant ( $P > 0.05$ ) following Bonferroni correction.

<sup>a</sup>*t* test.

<sup>b</sup>Two-sample *Z* test for proportions.

marked by moose, however, had a much larger dbh (7.9 cm) than did unmarked willows (2.7 cm). This outcome was probably the reason we failed to detect an overall difference in the dbh's of marked and unmarked trees when all species were combined (Table 1). Moose also selected trees to scent mark that had a relatively low first branch and smooth bark (Table 1). Moose clearly preferred trees of a particular species and with particular morphological characteristics for scent marking, but the locations of these trees were not clumped.

In addition to many trees with dead tops (Table 1), trees scent marked by moose ( $N = 54$ ) had the following characteris-

tics. The diameter of the tree at the midpoint of the scraped bark was  $7.5 \pm 5.6$  cm and the length of the scrape was  $46.9 \pm 28.5$  cm. The midpoint of the scrape was  $115.6 \pm 28.1$  cm above the substrate, and the distance between unbroken branches encompassing the scrape was  $90.4 \pm 31.2$  cm.

### Discussion

Our observations confirm that like other genera of cervids in North America (*Cervus*, *Odocoileus*, *Rangifer*), *Alces* scent marks trees and shrubs (i.e., engages in sign-posting behavior

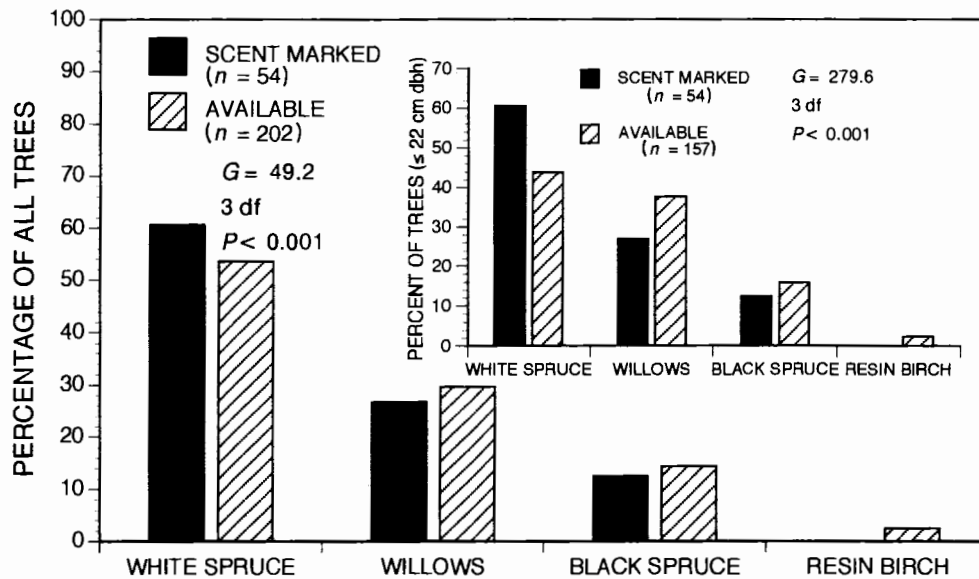


FIG. 2. Percentages of trees scent marked by Alaskan moose relative to the percentage of trees available, interior Alaska, U.S.A., 1989.

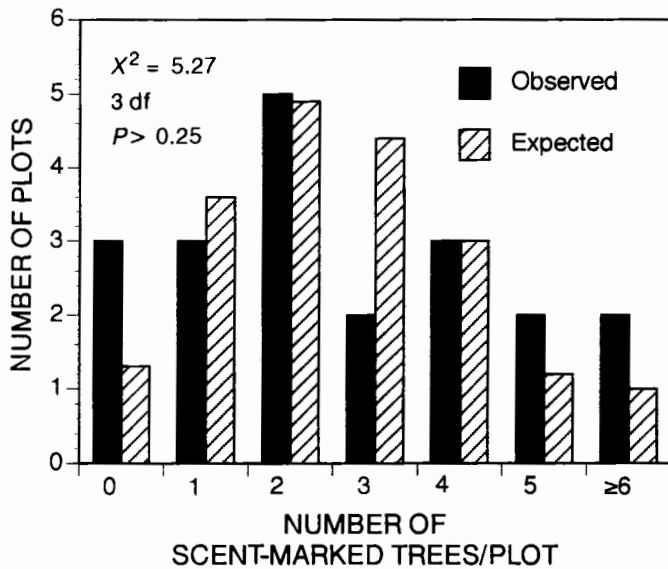


FIG. 3. Observed distribution of trees scent marked by Alaskan moose on sample plots compared with a random (Poisson) distribution, interior Alaska, U.S.A., 1989.

that involves the rubbing of trees). Indeed, such behavior may be widespread in the Cervidae (Putman 1988; Shea et al. 1990). This behavior is completely different from the debarking of some trees and shrubs for food, which tends to occur in winter in temperate and arctic environments, and may indicate a localized shortage of food (Murie 1934; Miquelle and Van Ballenberghe 1989). We never observed either male or female moose eating the bark that was stripped from trees while engaging in scent marking. Moose seldom feed on white spruce (Van Ballenberghe et al. 1989), although they selected this species for scent marking (Fig. 2). Moreover, the rubbing of the head on the scrape cannot be explained if moose performed this behavior to feed.

In at least some genera of cervids, the stripping of bark and rubbing of trees is typically associated with antler thrashing by males (Fuchs 1977; Bowyer 1986; Putman 1988). Bark strip-

ping without antler thrashing, however, occurs in male elk (*Cervus elaphus*; Bowyer and Kitchen 1987), and this also is the case for Alaskan moose. Both male and female moose scent marked trees, which also occurs in elk (Bowyer and Kitchen 1987) and white-tailed deer (Marchinton et al. 1990). In elk, however, scent marking of trees occurs throughout the year (Bowyer and Kitchen 1987), whereas in moose it occurs at the peak of rut for females and during late or postrut for males.

Where antler thrashing and the stripping of bark and rubbing of trees with the head are linked, it is reasonable to assume that such behavior conveys information about a male's dominance: among these cervids, antler thrashing is a dominance display (Bowyer and Kitchen 1987). Further, such behavior is unrelated to removal of velvet from the antlers, because such displays continue long after velvet shedding is completed (Kile and Marchinton 1977; Bowyer 1986; Benner and Bowyer 1988). Where antler thrashing and subsequent scent marking are not coupled, however, the interpretation is less straightforward. The timing of tree rubbing in moose suggests that it is rut related, and our observations of aggression over freshly marked trees indicate that the function of such marks is ephemeral. We believe that this behavior incorporates both visual and olfactory cues. Moose would not likely rub the bark-stripped area with their head if scent were not being deposited. Other cervids (Volkman et al. 1978) possess a glandular forehead, but whether moose have such glands is unknown.

Kile and Marchinton (1977) postulated that white-tailed deer selected aromatic species of trees for scent marking. This may explain, in part, why moose selected the more aromatic white spruce over willows, black spruce or resin birch for rubbing (Fig. 2). Certainly, the strong odor of a freshly marked tree might add an olfactory signal to any pheromones deposited and enhance visual cues to attract conspecifics. Also, many white spruce were of an overall size and growth form preferred by moose for rubbing.

Some ungulates (Gilbert 1973; Gosling 1982, 1987) may delineate their territories by scent marking, but available evidence suggests moose are not territorial (Van Ballenberghe and Miquelle 1993). Indeed, many nonterritorial mammals

scent mark (Ralls 1971). In addition, if moose were territorial, we would expect scent-marked trees to have been clumped within or around territories, although such clumping of marks alone might not be sufficient to determine whether moose are territorial. Even though the trees available to mark possessed a clumped distribution, the trees that moose scent marked were not spatially clumped (Fig. 3). Behavioral observations of moose during rut (Peek et al. 1986; Van Ballenberghe and Miquelle 1993), the lack of a clumped distribution of rubbed trees, and the ephemeral nature of these marks makes it unlikely that scent marking is related to territoriality in this cervid.

What, then, might be the function of scent marking of trees by moose? Bowyer and Kitchen (1987) hypothesized that elk marked trees (scent posts) to help orient and familiarize themselves with their environment. Such behavior occurred among all sex and age classes of elk and was observed throughout the year (Bowyer and Kitchen 1987). The marking of trees by moose, however, was associated with rut; this leads us to believe that rubbing of trees is related to dominance, mating, or both. Even though moose behaved aggressively over possession of scent-marked trees, it is difficult to relate this behavior solely to dominance status because males did not rub trees until late in rut, when dominance relationships would have been well established (Peek et al. 1986; Van Ballenberghe and Miquelle 1993).

Because females marked trees at the peak of rut, when most were in estrus, we postulate that this behavior is related to mating. Male moose dig and urinate in rutting pits that ostensibly function to prime estrus in females (Miquelle et al. 1990). Might the marking of trees by females signal the presence of a female in estrus? Moose evolved in the dense boreal forests of Eurasia (Peterson 1955), and ungulates living in closed habitats would be expected to rely extensively on olfaction for communication (Müller-Schwarze 1983). Moreover, boreal forests tend to be less productive than many other habitats (Telfer 1984), and moose often occur at low densities in areas where a full complement of natural predators is present (Gasaway et al. 1992). Under such conditions, finding a mate might be difficult, and it would be highly adaptive for males and females to synchronize mating activities; late-born young are at a substantial disadvantage in northern ecosystems, and recycling into a second estrus because a female did not initially find a mate would substantially delay the birth of young (Schwartz and Hundertmark 1993). We hypothesize that the marking of trees functions to communicate the presence of estrous females to males. The strong visual cue of a marked tree and associated olfactory signal would serve such a function well. Unlike some cervids, female moose exhibit few other overt behaviors associated with estrus (Schwartz and Hundertmark 1993; Van Ballenberghe and Miquelle 1993). Moreover, this hypothesis is consistent with the timing of tree rubbing by females (Van Ballenberghe and Miquelle 1993); nonetheless, additional behavioral observations will be necessary to critically test this idea.

Miquelle (1991) proposed that male moose attract females to rutting pits by scent marking these areas with their urine, which contains a pheromone that likely primes estrus. Such behavior slightly precedes the peak of rut and then wanes in early October (Miquelle 1991). Likewise, the strong smell of the urine deposited in rutting pits subsides as males begin feeding again in late September (Miquelle et al. 1990). Whatever

the cause of hypophagia in rutting male moose, it is linked with the strong odor of urine deposited in rutting pits (Miquelle et al. 1990).

We hypothesize that the marking of trees by male moose late in rut serves a similar function to rutting pits: it attracts females not successfully bred during peak rut. Such behavior might also help prime estrus in these females. This interpretation is consistent with the timing of events and behavioral observations of scent marking. Again, however, additional behavioral analyses will be required to test this idea.

Our hypothesis concerning the function of scent marking of trees by moose has several strengths: it explains the differential timing of marking between the sexes, it is consistent with behavioral observations, and it is in keeping with what is known about other types of scent marking by moose. Finally, it provides a similar explanation of this behavior for males and females: advertising the presence of a reproductively receptive mate (and perhaps priming estrus in females). More data are required to test this idea, but we believe that research designed to investigate this potential function of scent marking should be pursued.

#### Acknowledgments

We thank the personnel of Denali National Park and Preserve for their assistance during our fieldwork. We thank J.L. Rachlow and M. Petrula for help with sampling trees. E.C. Murphy and D. Person offered statistical guidance for which we are grateful, and B.D. Bowyer provided Figs. 2 and 3. Funding for this project was provided by the U.S. Department of Agriculture Forest Service and the Institute of Arctic Biology at the University of Alaska Fairbanks (UAF). All procedures used in this research were approved by an independent Animal Care and Use Committee at UAF.

- Atkeson, T.D., and Marchinton, R.L. 1982. Forehead glands in white-tailed deer. *J. Mammal.* **63**: 613–617.
- Benner, J.M., and Bowyer, R.T. 1988. Selection of trees for rubs by white-tailed deer in Maine. *J. Mammal.* **69**: 624–627.
- Bossert, W., and Wilson, E.O. 1963. An analysis of olfactory communication among animals. *J. Theor. Biol.* **5**: 443–469.
- Bowyer, R.T. 1986. Antler characteristics as related to social status of male southern mule deer. *Southwest. Nat.* **31**: 289–298.
- Bowyer, R.T., and Kitchen, D.W. 1987. Significance of scent-marking by Roosevelt elk. *J. Mammal.* **68**: 418–423.
- Coblentz, B.F. 1976. Functions of scent-urination in ungulates with special reference to feral goats (*Capra hircus*). *Am. Nat.* **110**: 549–557.
- de Vos, A. 1967. Rubbing of conifers by white-tailed deer in successive years. *J. Mammal.* **48**: 146–147.
- de Vos, A., Brokx, P., and Geist, V. 1967. A review of social behavior of the North American cervids during the reproductive period. *Am. Midland Nat.* **77**: 390–417.
- Eisenberg, J.F., and Kleiman, D.G. 1972. Olfactory communication in mammals. *Annu. Rev. Ecol. Syst.* **3**: 1–32.
- Ewer, R.F. 1968. *Ethology of mammals*. Plenum Press, New York.
- Flood, P.F., Abrams, S.R., Muir, G.D. and Rowell, J.E. 1989. Odor of the muskox: a preliminary investigation. *J. Chem. Ecol.* **15**: 2207–2217.
- Fuchs, E.R. 1977. *Behavior*. Kleberg Studies in Natural Resources, Texas A&M University, College Station. pp. 24–52.
- Gasaway, W.D., Boertje, R.D., Grangaard, D.V., Kellyhouse,

- D.G., Stephenson, R.O., and Larsen, D.G. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildl. Monogr.* No. 120.
- Geist, V. 1963. On the behavior of the North American moose (*Alces alces andersoni* Peterson 1950) in British Columbia. *Behaviour*, **20**: 377–416.
- Geist, V. 1966. Ethological observations on some North American cervids. *Zool. Beitr. (n.s.)*, **12**: 219–250.
- Gilbert, B.K. 1973. Scent marking and territoriality in pronghorn (*Antilocapra americana*) in Yellowstone Park. *Mammalia*, **37**: 25–33.
- Gleason, K.K., and Reynierse, J.H. 1969. The behavioral significance of pheromones in vertebrates. *Psychol. Bull.* **71**: 58–75.
- Gosling, L.M. 1982. A reassessment of the function of scent marking in territories. *Z. Tierpsychol.* **60**: 89–118.
- Gosling, L.M. 1985. The even-toed ungulates: order Artiodactyla. Sources, behavioral context, and function of chemical signals. In *Social odours in mammals*. Edited by R.E. Brown and D.W. MacDonald. Oxford University Press, Oxford, U.K.
- Gosling, L.M. 1987. Scent marking in an antelope lek territory. *Anim. Behav.* **35**: 620–622.
- Johnson, R.P. 1973. Scent marking in mammals. *Anim. Behav.* **21**: 521–535.
- Kennaugh, J.H., Chapman, D.I., and Chapman, N.G. 1977. Seasonal changes in the prepuce of adult fallow deer (*Dama dama*) and its possible function as a scent organ. *J. Zool. (1965–1984)*, **183**: 301–310.
- Kershaw, K.K. 1964. Quantitative and dynamic ecology. Edward Arnold, London.
- Kile, T.L., and Marchinton, R.L. 1977. White-tailed deer rubs and scrapes: spatial, temporal and physical characteristics and social role. *Am. Midl. Nat.* **97**: 257–266.
- Lent, P.C. 1974. A review of rutting behavior in moose. *Natr. Can.* **101**: 307–323.
- Marchinton, R.L., and Hirth, D.H. 1984. Behavior. In *White-tailed deer ecology and management*. Edited by L.K. Halls. Wildlife Management Institute and Stackpole Books, Harrisburg, Pa.
- Marchinton, R.L., Johansen, K.L., and Miller, K.V. 1990. Seasonal variation in marking behavior of white-tailed deer. In *Chemical signals in vertebrates*. Edited by D.W. MacDonald, D. Muller-Schwarze, and S.E. Natynczuk, Oxford University Press, Oxford, U.K. pp. 295–301.
- McCullough, D.R. 1969. The tule elk: its history behavior and ecology. *Univ. Calif. Publ. Zool.* **88**: 1–209.
- Miquelle, D.G. 1991. Are moose mice? The function of scent urination in moose. *Am. Nat.* **138**: 460–477.
- Miquelle, D.G., and Van Ballenberghe, V. 1989. Impact of bark stripping on aspen–spruce communities. *J. Wildl. Manage.* **53**: 577–586.
- Miquelle, D.G., Peek, J.M., and Van Ballenberghe, V. 1990. Why don't bull moose eat during the rut? *Behav. Ecol. Sociobiol.* **27**: 145–151.
- Miquelle, D.G., Peek, J.M., and Van Ballenberghe, V. 1992. Sexual segregation in Alaskan moose. *Wildl. Monogr.* No. 122.
- Miller, K.V., Kammermeyer, K.E., Marchinton, R.L., and Moser, B.E. 1987. Population and habitat influences on antler rubbing by white-tailed deer. *J. Wildl. Manage.* **51**: 62–66.
- Molvar, E.M., Bowyer, R.T., and Van Ballenberghe, V. 1993. Moose herbivory, browse quality, and nutrient cycling in an Alaskan treeline community. *Oecologia*, **94**: 472–479.
- Moore, W.G., and Marchinton, R.L. 1974. Marking behavior and its social function in white-tailed deer. In *The behavior of ungulates and its relation to management*. Edited by V. Geist and F. Walther. Publ. No. 24 (n.s.), International Union for Conservation of Nature and Natural Resources, Morges, Switzerland.
- Müller-Schwarze, D. 1971. Pheromones in black-tailed deer (*Odocoileus hemionus columbianus*). *Anim. Behav.* **19**: 141–152.
- Müller-Schwarze, D. 1972. Social significance of forehead rubbing in black-tailed deer (*Odocoileus hemionus columbianus*). *Anim. Behav.* **20**: 788–797.
- Müller-Schwarze, D. 1983. Scent-glands in mammals and their functions. In *Advances in the study of mammalian behavior*. Edited by J.F. Eisenberg and D.G. Kleiman. *Am. Soc. Mammal. Spec. Publ. No. 7*. pp. 150–197.
- Müller-Schwarze, D., Kallquist, L., Mousing, L., Brundin, T., and Anderson, G. 1978a. Responses of reindeer to interdigital secretions of conspecifics. *J. Chem. Ecol.* **4**: 325–335.
- Müller-Schwarze, D., Ravid, U., Claesson, A., Singer, A.G., Silverstein, R.M., Muller-Schwarze, C., Volkman, N.J., Zemanek, K.F., and Butler, R.G. 1978b. The “deer lactone”: source, chiral properties, and responses by black-tailed deer. *J. Chem. Ecol.* **4**: 247–256.
- Murie, A. 1934. The moose of Isle Royale. *Misc. Publ. Mus. Zool. Univ. Mich.* No. 25.
- Nielsen, D.G., Dunlap, M.J., and Miller, K.V. 1982. Pre-rut rubbing by white-tailed bucks: nursery damage, social role, and management options. *Wildl. Soc. Bull.* **10**: 341–348.
- Odend'hal, S., Miller, K.V., and Hoffmann, D.M. 1992. Preputial glands in the white-tailed deer (*Odocoileus virginianus*). *J. Mammal.* **73**: 299–302.
- Peek, J.M., Van Ballenberghe, V., and Miquelle, D.G. 1986. Intensity of interactions between rutting bull moose in central Alaska. *J. Mammal.* **67**: 423–426.
- Peters, R. 1980. Mammalian communication: a behavioral analysis of meaning. Brooks-Cole, Monterey, Calif.
- Peterson, R.L. 1955. North American moose. University of Toronto Press, Toronto.
- Putman, R. 1988. The natural history of deer. Comstock Publishing Associates, Cornell University Press, Ithaca, N.Y.
- Quay, W.B. 1959. Microscopic structure and variation in the cutaneous glands of the deer (*Odocoileus virginianus*). *J. Mammal.* **40**: 114–128.
- Quay, W.B., and Muller-Schwarze, D. 1970. Functional histology of integumentary glandular regions in black-tailed deer (*Odocoileus hemionus columbianus*). *J. Mammal.* **51**: 675–694.
- Ralls, K. 1971. Mammalian scent marking. *Science (Washington, D.C.)*, **171**: 443–449.
- Remington, R.D., and Schork, M.A. 1970. Statistics with applications to the biological and health sciences. Prentice-Hall, Englewood Cliffs, N.J.
- Rice, W.R. 1989. Analyzing tables of statistical tests. *Evolution*, **43**: 223–225.
- Schwartz, C.C., and Hundertmark, K.J. 1993. Reproductive characteristics of Alaskan moose. *J. Wildl. Manage.* **57**: 454–468.
- Shea, S.M., Flynn, L.B., Marchinton, R.L., and Lewis, J.C. 1990. Part II. Social behavior, movement ecology, and food habits. In *Ecology of sambar deer on St. Vincent National Wildlife Refuge, Florida*. Bull. No. 25, Tall Timbers Research Station, Tallahassee.
- Tanton, T.L. 1920. Depressions found on moose trails and their significance. *J. Mammal.* **1**: 142–143.
- Telfer, E.S. 1984. Circumpolar distribution and habitat requirements of moose (*Alces alces*). In *Northern ecology and resource management*. Edited by R. Olsen, R. Hastings, and F. Geddes. University of Alberta Press, Edmonton. pp. 145–182.
- Thiessen, D.D., and Rice, M. 1976. Mammalian scent marking and social behavior. *Psychol. Bull.* **83**: 505–539.
- Thompson, W.L. 1949. Observations of moose courting behavior. *J. Wildl. Manage.* **13**: 313.
- Van Ballenberghe, V. 1992. Behavioral adaptations of moose to tree-line habitats in subarctic Alaska. *Alces Suppl.* No. 1. pp. 193–206.
- Van Ballenberghe, V., and Miquelle, D.G. 1993. Mating in moose: timing, behavior, and male access patterns. *Can. J. Zool.* **71**: 1687–1690.
- Van Ballenberghe, V., Miquelle, D.G. and MacCracken, J.G. 1989. Heavy utilization of woody plants by moose during summer at Denali National Park, Alaska. *Alces*, **25**: 31–35.

- Volkman, N.J., Zemanek, K.F., and Müller-Schwarze, D. 1978. Antorbital and forehead secretions of black-tailed deer (*Odocoileus hemionus columbianus*): their role in age-class recognition. *Anim. Behav.* **26**: 1098–1100.
- Wemmer, C.M., and Murtaugh, J. 1980. Olfactory aspects of rutting behavior in the bactrian camel (*Camelus bactrianus ferus*). In *Chemical signals: vertebrates and aquatic invertebrates*. Edited by D. Müller-Schwarze and R.M. Silverstein. Plenum Press, New York, pp. 107–124.
- Whitaker, R.H. 1975. *Communities and ecosystems*. MacMillan Publishing Co., New York.
- Woodin, H.E. 1956. The appearance of a moose rutting ground. *J. Mammal.* **37**: 458–459.