

ARE MOOSE MICE? THE FUNCTION OF SCENT URINATION IN MOOSE

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Abstract.—Scent urination likely serves a variety of functions, depending on the species and environment in which it is expressed. Evidence derived from observations in Denali National Park and Preserve (DNPP) suggests that scent urination by bull moose (*Alces alces*) is primarily directed toward females and supports the hypothesis that scent urination induces ovulation in cows. Testing of this hypothesis should be possible in captive populations. Males also appear to use urine as a means of attracting females. Female competition for a male resource is rare in mammalian mating systems, yet cow moose in DNPP aggressively compete for access to bull urine, suggesting that male urinary components may increase the probability of successful reproduction. While priming pheromones may be required by cows to ensure birthing when calf survival will be highest, whether or not bulls produce such pheromones may be dependent on the relative benefits accrued to them. Mature bulls that scent urinate may increase reproductive success by inducing ovulation before their body condition declines and attracting cows by their scent so that courtship is possible. Subadult bull moose do not scent urinate yet attempt to acquire some of its benefits by obtaining attractive odors from mature bulls. The evolution of scent urination as an important component of moose breeding behavior may be related to the evolution of moose in the circumpolar boreal forests. Females in low-density populations may increase reproductive success by being assured of the presence of a breeding bull before ovulation. Use of scent urination as a mechanism to time breeding appears to be one facet of an ecological opportunist strategy employed by moose to exploit environments that are either low quality (mature boreal forests) or temporary and unpredictably distributed (seral shrub communities).

During the breeding season many male ungulates use urine as a medium to transmit information to conspecifics. Scent urination, or impregnation of pelage with urine (Coblentz 1976), is most commonly performed by males in Cervidae (Espmark 1964; Kennaugh et al. 1977; Geist 1981a; Wemmer et al. 1983; Bowyer and Kitchen 1987) and Caprinae (Shank 1972; Coblentz 1976). Males usually scent urinate by urinating directly onto themselves, but some species urinate onto the ground and then lie or wallow in the urine (Geist 1964; Fuchs 1977; Bowyer and Kitchen 1987). These wallows remain available to other animals, providing the opportunity for use, investigation, or assessment. Urine of males that scent urinate has a strong odor to humans (Lincoln 1971; Shank 1972; Coblentz 1976; Bowyer and Kitchen 1987), and Kennaugh et al. (1977) provided evidence that the prepuce produces the pungent odor in urine of male fallow deer (*Dama dama*).

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Thus, scent urination could presumably transmit information in several ways: scent urination could act as a visual display, a wallow site could act as both a visual and olfactory signal, and the odor imparted to an animal through scent urination could act as an olfactory signal.

Coblentz (1976) reviewed information on scent urination and outlined a set of hypotheses to explain its role in intraspecific communication in ungulate species. This article addresses four of these hypotheses and tests three by comparing empirical observations and expected behaviors of moose during the rut. A synthetic approach used by Bronson (1979) to understand the reproductive ecology of the house mouse (*Mus musculus*) was used to consider the ecological context of scent urination in moose (*Alces alces*) and other ungulates.

Hypothesized Functions of Scent Urination

1. *The rank-symbol hypothesis.*—Shank (1972) proposed that scent urination acted as an “olfactory rank symbol,” with the strength of the scent (or possibly particular metabolites) acting as an agonistic message directed toward other males. High-ranking males could reduce energy expenditure and the probability of injury while retaining dominance by advertising their high status. However, as Barrette and Vandal (1986) noted, dominance is not an attribute of an individual: it is an attribute of a relationship between two animals. If individual males have not previously interacted (which is likely in many populations of ungulates), it seems unlikely that specific rank or complicated hierarchical information could be conveyed by differences in scent (Bowyer and Kitchen 1987). Olfactory cues would more plausibly convey information on status (e.g., a mature male ready to fight) by an indication of body condition, fighting ability, or endocrine state because many correlates of dominance are physical traits. Consequently, this hypothesis will not be considered further but is recast in a more plausible format as hypothesis 2.

2. *The physical-condition hypothesis.*—Some component of physical condition, which could be a correlate of dominance (Clutton-Brock and Albon 1979), may be advertised through urinary metabolic by-products (McCullough 1969). For example, urinary metabolites may signal fighting ability through physical condition and endocrine state. Males advertising good condition through scent urination could reduce time and energy invested in male-male interactions.

Coblentz (1976) suggested that, because many male ungulates reduce or stop feeding during the breeding season (Pollock 1975; McMillan et al. 1980; Miquelle 1990), metabolic by-products of fat catabolism may be the physiological pathway through which such signals are produced. Fat catabolism is unlikely to produce the odor associated with urine during scent urination: if such were the case, any animal dependent on fat catabolism (males in late winter, lactating females) would smell like a rutting male. However, the hypothesis is still reasonable if some other physiological process (perhaps associated with testosterone production) resulted in production of volatile metabolites in the urine.

3. *The masking hypothesis.*—Although scent urination may function primarily to advertise good physical condition, secondarily it may provide males an opportunity to mask a decline in condition or status. If males are able to assess condition via metabolites in the urine, changes in urine composition might be detectable

by competitors. Late in the breeding season it would be disadvantageous for males that have already expended large amounts of energy to advertise poor condition. Nonetheless, termination of scent urination may be as much an indicator of declining body condition as changes in metabolic by-products. Changes in urinary metabolites that might be detected by competitors could be concealed by other components that persisted throughout the rut. Coblenz (1976) proposed that the strong odor of male urine during the rut might act to mask declining body condition. Concealment of a decline may enable an animal to extend its breeding-status tenure.

4. *The primer hypothesis.*—Scent urination may be directed toward females, with male urinary compounds acting as priming pheromones to induce ovulation, as exemplified by the house mouse (Whitten 1956). Exposure of female mice to male urine results in luteinizing-hormone surges that trigger ovulation. Female mice exhibit a shorter estrous cycle when housed with a male than when isolated (Brown 1985).

Evidence from domestic and wild species suggests that priming pheromones may exist in some ungulates. Anestrous female goats exposed to males show signs of estrus within 5.5 d (Ott et al. 1980). Introduction of a Merino ram stimulated ovulation in ewes (Watson and Radford 1960; Oldham et al. 1979). Verme et al. (1987) reported that the date of breeding in captive white-tailed deer (*Odocoileus virginianus*) was 9 d earlier when does were continuously confined with bucks. The mechanism inducing ovulation in ungulates is not well-defined: odor of buck goats was not an important factor inducing ovulation in goats (Shelton and Morrow 1965), and ram sheep urine had no priming effect in sheep (Knight and Lynch 1980). Ovulation inducement through scent urination or scent marking has been postulated for fallow deer (Kennaugh et al. 1977), white-tailed deer (Miller et al., in press), and moose (Bubenik 1983).

Scent Urination by Moose

Scent urination by moose has been briefly described by a number of authors (Denniston 1956; M. Altmann 1959; Geist 1963; Miquelle and Van Ballenberghe 1985). During the rut, urine of bull moose has a strong, pungent odor (Flerov 1952; D. G. Miquelle, personal observation). Bull moose paw a shallow depression, known as a pit, in the ground, urinate into the depression, and then cover themselves with urine by splashing the urine-mud mixture onto themselves with their front hooves and/or lying (wallowing) in the urine. Cows also wallow in pits dug by bulls (Lent 1974; Miquelle and Van Ballenberghe 1985), and, on occasion, bulls use pits created by other bulls (see below). Any hypothesis attempting to explain the functional significance of scent urination should address the behavioral patterns of bulls creating pits, and of cows and other bulls visiting these pits (fig. 1).

Hypotheses Predictions for Moose

A set of predictions for moose behavior during the rut was generated for each of the three scent-urination hypotheses. These predictions can then be compared to empirical observations to determine which hypotheses are tenable.

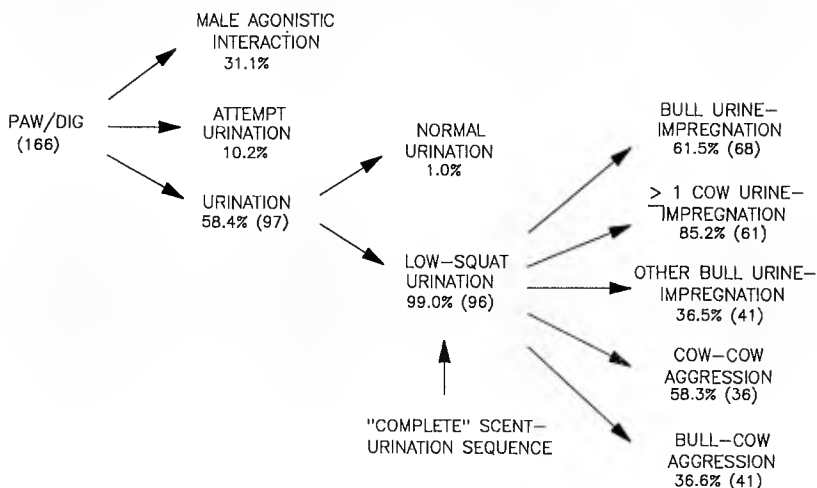


FIG. 1.—Sequence of behaviors associated with scent urination by moose. Occurrences are expressed as the percentage of observations during which a behavior was performed after the preceding behavior in the diagram. Percentages are based on sample sizes in parentheses. Sample sizes in right column are based on the number of observations during which that sex/social class was present.

The physical-condition hypothesis.—Male ungulates in northern temperate climates often make large energy investments during the short breeding season. This is reflected in a loss of fat and lowered body condition by the end of the rut (Flook 1970; Mitchell et al. 1976; Schwartz et al. 1987). With the exception of very old individuals, age and body and antler size are generally correlated with dominance (Clutton-Brock 1982; Bowyer 1986), and large-bodied, large-antlered, mature males generally invest most heavily in reproductive activities. As a result, body condition of mature males is likely to decline most rapidly during the course of a rutting season (McCullough 1969; Flook 1970; Clutton-Brock et al. 1982). If scent urination by bull moose acts to advertise physical condition during the rut, the following behaviors would be expected: (1) scent urination should be performed commonly by all bulls early in the rut, when all are in relatively good condition, but, as the rut progresses, mature bulls, most active in breeding and defending cows, should stop or reduce rates of scent urination as their body condition declines. (2) Smaller subadult bulls that have not been as active courting and defending cows should maintain or increase their rate of scent urination as their relative condition improves. (3) After a bull leaves a pit it has dug, the pit is available to other animals. Bulls in poor condition (e.g., mature bulls late in the rut) could cheat in the signal they convey by wallowing in pits of bulls in good condition (e.g., younger bulls). If scent urination provides a measure of fighting ability, then (4) only large bulls should scent urinate since small bulls cannot successfully compete with large bulls, and (5) the timing of scent urination should coincide with the time when fighting is most likely to occur.

The masking hypothesis.—Scent urination cannot function solely to mask

physical condition because the act of scent urination would itself signal a decline in condition. However, it may function primarily in another capacity (e.g., to advertise good physical condition), and secondarily to mask poor condition. Under these conditions, (1) scent urination should be maintained at a consistent level throughout the rut. An alternative means of masking body condition would be to wallow in pits of other bulls. If bulls attempt to hide declining condition with another animal's odor, then (2) large bulls (those most likely to experience a decline in body condition) should wallow in pits of younger bulls (those in better condition).

The male-oriented hypotheses.—Whether scent urination acts to advertise or mask physical condition, the first two hypotheses imply that information associated with scent urination is directed toward males. Males could obtain information from conspecifics by observing scent urination by competitors, smelling them directly, or locating and smelling pits in which potential competitors have urinated. Males that would profit most from information contained in pits should frequent them most often. Therefore, (1) if scent urination is a visual display directed toward males, it should be performed more commonly in the presence of males than females, and (2) if a pit contains information directed toward male competitors, bulls should assess one another's condition by visiting pits (directly approaching competitors for olfactory assessment may be misinterpreted as a challenge), whereas cows should be uninterested in pits (unless females use the information in mate choice). Males capable of gaining status should be most interested in visiting pits of competitors. Because younger, smaller animals are rarely capable of successfully challenging older, larger bulls (Clutton-Brock et al. 1979; Peek et al. 1986), males should express interest in pits created by bulls of approximately the same size. Assessment would likely be possible simply by smelling the pit.

The primer hypothesis.—Because date of birth can be a critical factor affecting survival of young in northern ungulates (Rutberg 1987; Festa-Bianchet 1988), date of breeding can affect reproductive success. Large bulls would gain an advantage by inducing cows to ovulate early in the rut before their body condition declines and their status is challenged. Small bulls that are unable to defend cows from larger competitors gain little from ovulation inducement. Females could regulate timing of ovulation by timing an interest in pits and an attraction to the odor of bull urine. Females could "acquire" priming pheromones from pits created by males or directly from males that have scent urinated. Simply smelling pits or males that scent urinate might be adequate, but impregnation of their own pelage with male urine likely would be more effective by creating a temporary "cloud" of pheromones surrounding the female. Urine impregnation by females could occur in two ways: splashing and wallowing in pits created by males, or rubbing against males that scent urinate.

If scent urination acts to induce ovulation, (1) scent urination should be performed before breeding, and (2) scent urination should be commonly performed by large bulls early in the rut, but rarely by small bulls. Because timing of pregnancy is important, it would be advantageous for females to (3) express interest in pits, (4) impregnate themselves with urine by wallowing in pits or rubbing

against males that scent urinate, (5) compete, if necessary, with other females for access to pits, and (6) express greater interest in bulls that scent urinate than those that do not. If females are attracted only to urine of bulls that scent urinate, (7) "cheating" (urine impregnation in another bull's pit) by bulls that do not scent urinate may be advantageous. Finally, (8) ovulation should be later in females not exposed to bull urine.

METHODS

Study Area and Mating System

Moose were observed in the northeast corner of Denali National Park and Preserve (DNPP), Alaska, in a broad valley bordered on the south by the Alaska Range and on the north by a secondary range. Moose occur in black and white spruce (*Picea mariana* and *Picea glauca*) forests below 800 m, and in dense shrub communities of willow (*Salix* spp.) and resin birch (*Betula glandulosa*) up to 1,100 m. Moose are not hunted in DNPP and are tolerant of observers in close proximity.

Cows in DNPP form aggregations during the rut, and bulls aggressively attempt to monopolize breeding access to these groups (D. G. Miquelle, V. Van Ballenberghe, and J. M. Peek, unpublished manuscript). This breeding system is unusual in comparison to other moose populations, in which cows are normally solitary throughout the rut (Flerov 1952; M. Altmann 1959; Geist 1963).

Data Collection

Observations of moose, made between August 25 and October 10, 1981–1983, and 1986, were separated by date into three periods that coincided with phases of the rut. During period 1, August 25–September 10, velvet was shed from antlers (Van Ballenberghe 1983) and bulls commonly aggregated. During period 2, September 11–25, bulls defended and courted cows. Period 3, September 26–October 10, was considered the peak of the rut because 97% of all observed copulations occurred during this period (see below).

Bulls were separated into four size classes on the basis of antler and body size: yearlings were small-bodied animals with nonpalmate, or very small palmate, antlers; class 1 bulls were small animals with antler spreads <100 cm; class 2 bulls had antler spreads between 100 and 155 cm; class 3 bulls were largest in body size and had antler spreads >155 cm. These classifications, based on visual assessments, were supported by actual measurements of drugged animals and differences among size classes in the total number of antler tines (D. G. Miquelle, unpublished data). Yearlings and class 1 bulls were combined for some analyses as small bulls; class 2 and 3 bulls were combined as large bulls. Because body and antler size are positively correlated with age in moose (Sæther and Haagenrud 1985; Gasaway et al. 1987), these categories are representative of broad age classes (subadult and mature bulls).

Bulls were considered part of a group if located within 100 m of another moose. Group types were defined as lone bulls, bull-only groups, one bull-cow (one bull, one or more cows), or multi-bull-cow (more than one bull, one or more cows).

TABLE 1
RATE OF BULL MOOSE SCENT URINATION
BY SIZE CLASS AND SOCIAL GROUP

Variable Class	n^*	Scent-Urination Rate† (acts/h)
Size class:‡		
Yearlings	17	.00
Class 1	34	.03
Class 2	54	.14
Class 3	70	.15
Social group:§		
Lone bulls	6	.33
Bull-only	18	.13
One bull-cow	39	.15
Multi-bull-cow#	148	.15

* Each sampling unit (n_i) equals total active time spent by bulls in each size class observed in one group during 1 d. Based on 14,856 min of bull moose activity.

† Pit dug and urinated in by bull.

‡ Size classes were based on antler and body size.

§ Based on large bulls (classes 2 and 3) only.

|| One bull, one or more cows.

More than one bull, one or more cows.

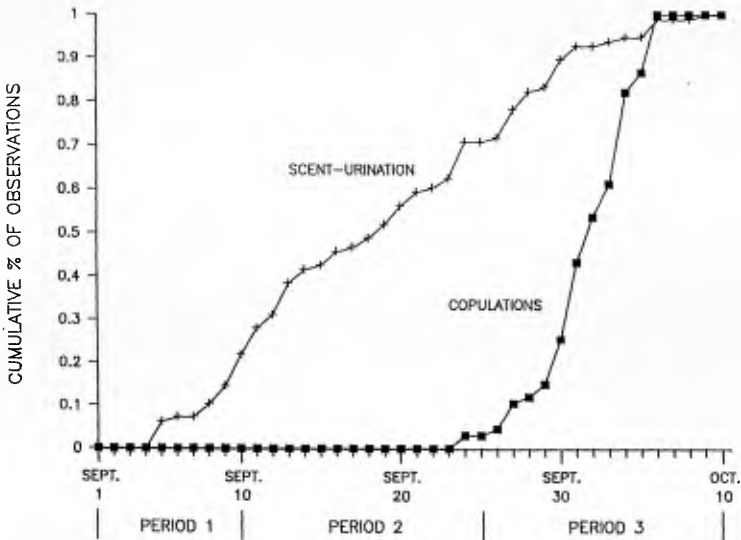


FIG. 2.—Cumulative percentage of observations of scent urination and copulations by moose in Denali National Park and Preserve, Alaska, 1981–1983 and 1986.

Data on scent urination were collected using focal-group sampling and an all-occurrences log (J. Altmann 1974) by observing groups within 100 m. Data on rates of aggression and scent urination were recorded as behavioral acts per active hour (Kucera 1978; Bowyer 1981). Observations of one group over the course of 1 d were considered a sampling unit. The dates of all observed copulations and fights (Miquelle 1990) were recorded to compare to the timing of scent urination.

Goodness-of-fit log-likelihood ratios (*G*-test) were used to compare observed and expected frequencies of behaviors on the basis of the amount of observation time for each sex and size class or group type. The Kruskal-Wallis test was used to assess how cow responses to scent urination varied with group size. The Mann-Whitney *U*-test compared median dates of scent urination to those of copulation and fighting. A paired *t*-test was used to compare the rate of aggression between cows before and after scent urination by bulls.

RESULTS

Behavioral Sequences, Timing of Scent Urination, Copulation, and Fighting

During the period of study, 105 bulls were identified within the study site: of these, 37 were observed to scent urinate. Bulls initiated sequences of scent urination by pawing the ground, alternately digging with both front hooves. Pawing was associated with agonistic interactions between bulls (Walther 1984) as well as digging of pits (fig. 1). Pit digging often was interrupted when a bull assumed a low-squat urination posture (front legs stiff, hindquarters crouched low to the ground). Moose normally urinated into a pit only once but assumed the low-squat posture an average 2.6 ± 0.6 ($n = 52$) times before actually urinating. In between low-squat postures, bulls resumed digging the pit. A "complete" behavioral sequence for scent urination included pit digging and a low-squat urination into the pit (fig. 1). Bulls did not urinate 10% of the times they dug a pit and assumed the low-squat position (fig. 1).

Bulls covered themselves with urine 61.8% of the times they urinated in pits (fig. 1), using their front hooves to splash themselves with urine 61.8% of the time and wallowing in pits 45.6% of the time.

Class 2 and 3 bulls scent urinated at a similar rate (table 1). Scent urination was rare in class 1 bulls and was not observed in yearlings. Urine of small bulls (yearlings and class 1 bulls) had little or no smell to humans, while that of large bulls (classes 2 and 3) possessed a strong, pungent odor. Frequency of scent urination by class 2 and 3 bulls was independent of the type of group with which they associated (table 2; $G = 1.216$, $P > .5$).

Observations of scent urination by class 2 and 3 bulls were most common in period 2 (51.2%; $G = 11.55$, $P < .01$), with approximately equal occurrences in periods 1 (22.6%) and 3 (26.2%). Nearly all copulations (97%; $n = 68$) were observed in period 3 (fig. 2). The median date of scent urination (September 19; $n = 96$) was significantly earlier than the median date of copulations (October 2; Mann-Whitney test, $Z = 8.73$, $P = .0001$) and that of fights (September 28;

TABLE 2
 SIZE OF BULLS RESPONDING TO PITS
 CREATED BY ANOTHER BULL

	BULL SIZE*	
	Small	Large
Response†	21	9
No response	11	16
Total	32	25

* Small bulls are yearlings and class 1 bulls; large bulls are class 2 and 3 bulls.

† Minimum recorded response was for a bull to approach a pit.

$Z = 3.30$, $P = .001$). Most fights occurred in period 3 during the peak of breeding (Miquelle 1990).

Bull Responses to Scent Urination

Small bulls were more likely to respond to a pit made by another bull than were large bulls (table 2; $G = 5.01$, $P = .025$). When bulls reacted to scent urination by another bull ($n = 30$), they would (1) approach the pit (23.3%), (2) approach and smell the pit (23.3%), or (3) approach and impregnate themselves with urine of the other bull (53.3%). Wallowing in another bull's urine was done almost exclusively (14 of 15 occurrences) by small bulls and was most prevalent in period 2 (53.3%). Large bulls that created pits aggressively attempted to prevent small bulls from using their pits (54.5% of approaches; $n = 33$).

Cow Responses to Scent Urination

Cows were observed digging in pits created by bulls but never dug new pits, as reported by Bubenik (1987). Cows impregnated themselves with bull urine by splashing or wallowing in 85% ($n = 61$) of the pits created in their presence (fig. 1). If bulls did not urinate in pits, neither bulls nor cows splashed or wallowed ($n = 17$). Activity at pits was greatest immediately after bulls urinated in them. Despite obvious excitement exhibited by cows when bulls urinated in pits, their interest was difficult to assess quantitatively because bulls aggressively chased cows from pits 37% of the time, and aggressive interactions between cows over access to pits were common (fig. 1). Nonetheless, 50% (median; $n = 53$) of the cows present when a bull scent urinated at least approached the pit. Response varied with group size: cows in small groups (fewer than 6 cows) were more likely to approach pits (75% of cows present) than cows in medium-sized (6–10 cows; 53%) or large groups (more than 10 cows; 33%; $H = 10.14$, $n = 53$, $P = .006$). Response differences appeared to be due to cow aggression at pits. The rate of cow aggression 20 min before versus 20 min after bulls urinated in a pit showed a fivefold increase from 0.7 ± 0.6 to 3.8 ± 1.6 agonistic acts/active hour (paired $t = 3.30$, $df = 13$, $P = .006$).

TABLE 3
COW MOOSE BEHAVIORS DIRECTED TOWARD BULLS

	BULL SIZE*	
	Small	Large
Association time with cows (h)†	61.8	161.2
Cow smells bull	12	20
Cow rubs on bull	2	37

* Small bulls are yearlings and class 1 bulls; large bulls are class 2 and 3 bulls.

† Observation time during which bulls were active and associated with cows.

Cow moose rubbed against bulls (table 3), apparently in attempts to impregnate themselves with bull urine. Cows made nasal contact (apparently smelling) with large and small bulls in proportions expected, based on the amount of time large and small bulls associated with cows ($G = 1.43$, $P > .1$), but preferentially rubbed on large bulls ($G = 13.39$, $P < .001$); cows directed 95% of all observed rubbing sequences toward large bulls.

DISCUSSION

Comparison of Observed and Predicted Behaviors

The physical-condition hypothesis.—Predictions generated from this hypothesis were that all bulls should scent urinate commonly early in the rut, large bulls should stop earlier as their body condition declines, and small bulls should scent urinate more often later as their relative condition improves. Although scent urination by large bulls did decline in period 3, small bulls rarely scent urinated throughout the rut, contrary to predictions. Class 2 bulls, which were often relegated to satellite positions in groups, might gain an advantage by advertising late in the rut. Nevertheless, both class 2 and 3 bulls showed the same pattern in scent urination, with a peak in period 2, before the peak of the rut.

Bulls in poor condition could falsely advertise status by wallowing in pits created by bulls in good condition. The evidence, however, suggests that small bulls, which should be in relatively good condition, acquired odor from pits, whereas large bulls expressed little interest in other animals' pits.

Only large bulls scent urinated, as predicted if scent urination is an indicator of fighting ability. However, scent urination occurred earlier than the period when fighting was most common (Miquelle 1990), suggesting that scent urination may not signal fighting ability or readiness to fight. Most fights were observed during period 3, when males were intensely competing for access to females in estrus.

The masking hypothesis.—The prediction that scent urination should be maintained at a consistent level throughout the rut was contradicted since large bulls scent urinated less often in period 3. Large bulls, which should be in relatively poor condition later in the rut, did not wallow in other bulls' pits. Small bulls

that "cheated" by acquiring the scent of large bulls may have acted to mask their low status. However, dishonest advertisement of this form, which may lead to dangerous retaliation by larger, stronger opponents, and which is not based on an individual's physical attributes, is unlikely (Clutton-Brock and Albon 1979). However, acquisition of scent from mature bulls may have been an attempt by subadult bulls to gain a competitive advantage over other subadults rather than over larger males. If such were the case, large bulls should have been indifferent to use of their pits by subadults. Aggressive expulsion of smaller bulls from pits by large bulls weakens this line of argument.

The male-oriented hypotheses.—Scent urination should occur most often in the presence of individuals for which it was intended if it was a visual display. Scent urination was not preferentially performed in the presence of other bulls, suggesting that it was not an important visual display in bull-bull interactions. For a 2–3-wk period in mid-September, class 2 and 3 bulls were only observed urinating during the scent-urination behavioral sequence. Scent urination may simply occur when urination is necessary, independently of social context.

I predicted that bulls would benefit most by monitoring the condition of bulls approximately the same size. Since pits were dug almost exclusively by class 2 and 3 bulls, it was expected that bulls in these same classes would visit pits most often. But just the opposite occurred: small bulls were most likely to approach pits dug by large bulls. Bull behavior at another bull's pit did not appear to be associated with assessment: visitors usually attempted to acquire the scent at a pit by splashing or wallowing. Young bulls had little or no smell in their urine and were apparently attempting to acquire the odor of a larger bull.

Although these observations do not support the hypotheses that scent urination was directed toward bulls, in other ungulate species scent marking and scent urination appear to be important components of male agonistic interactions (Geist 1981a; Bowyer and Kitchen 1987; Miller et al. 1987). In these species, scent urination is often included as a component of dominance interactions and may occur immediately before fighting. Scent urination therefore appears to act as both a visual and olfactory signal in male-male interactions. In moose it appears that scent urination does not act as a visual signal directed toward competitors: scent urination did not temporally coincide with male agonistic interactions or precede fights. However, it is not possible to completely discount the importance of scent urination in bull moose interactions. Because the odor associated with scent urination is so strong, bulls may not need to observe scent urination by other bulls, visit pits, or closely approach other bulls to gain information about competitors. Responses to airborne olfactory cues over long distances (perhaps over 100 m) would be exceedingly difficult to quantify in field conditions. However, the available evidence suggests that scent urination does not play as prominent a role in male-male interactions as in other ungulate species. The strong reaction of cows to scent urination, in comparison to the response of other bulls, supports the hypothesis that scent urination is primarily female oriented.

The primer hypothesis.—Available evidence supports the predictions associated with the ovulation-inducement hypothesis. Scent urination was performed

before the peak of breeding in DNPP (fig. 2), as would be expected if urinary components induce ovulation. Large bulls dug pits most commonly early in the rut, while pit digging by small bulls was rare, as also was predicted.

Cow moose were extremely attracted to urine of bulls, impregnating their pelage by splashing and wallowing in pits with fresh bull urine, and rubbing against bulls. Interest was dramatically displayed by the high level of aggression exhibited among cows attempting to gain access to pits. Female competition for a male resource is extremely rare in ungulate breeding systems (Clutton-Brock et al. 1982; Gosling 1986) and suggests that exposure to bull urine may be a critical component of cow moose reproductive success.

Cow attraction to bull urine provided bulls with the opportunity to actively court cows that normally avoid bulls unless ready to breed (D. G. Miquelle, unpublished data). Subadult bulls can take advantage of such opportunities, despite their inability to produce strong-smelling urine, by smearing themselves with urine of mature bulls. Although cows preferred to rub against mature bulls, they smelled all bulls in expected proportions, perhaps as a means of assessment, and did express an interest in subadult bulls on occasion. Dishonest advertisement directed toward females would likely have little risk associated with it and could be used independently of body condition, unlike displays used to assess competitors (Clutton-Brock and Albon 1979). However, it would be expected that large bulls should try to prevent such dishonest advertisement by small bulls. Aggression exhibited by large bulls toward small bulls approaching pits supports this prediction.

Attempts by bulls to aggressively prevent cows from gaining access to pits were the only observed behaviors not clearly consistent with the primer hypothesis. Reasons for such aggression were not clear. Scent urination provides both bulls and cows with an opportunity for urine impregnation. Intersexual competition for initial access to the pit may explain male aggression. Once males were done wallowing, females almost always used pits. An alternative explanation is that bulls may intentionally prevent female access to pits because, without access, cows would be forced to rub against bulls to acquire priming pheromones, thereby providing bulls with courtship opportunities.

If bulls induce ovulation, the absence of bulls should result in a delayed initiation of estrus. This prediction was not tested in DNPP and would be difficult to test in a wild population. There is no information on ovulation dates of captive cow moose in the presence and absence of bulls and bull urine. A test of this prediction would be possible with captive animals.

Reproductive Ecology of Mice and Moose

Bronson (1979) suggested that the house mouse is a successful ecological opportunist because of a set of life-history and physiological traits. Feral mouse populations exist at relatively low densities, but dramatic increases are possible under good conditions. High dispersal potential increases the probability that temporary or new habitats will be found and exploited. A high reproductive rate provides opportunities for rapid exploitation of new resources. The pheromonal

priming system of mice aids in successful colonization and maintains high reproductive rates in low-density populations by promoting rapid ovulation when reproductively active males are present.

Moose share many of the characteristics that make mice successful ecological opportunists. Most moose populations are composed of solitary individuals existing at low densities in boreal forests, where forage biomass is low (Geist 1963; Krefting 1974; LeResche et al. 1974; Peek et al. 1974). Forest fires result in a localized resurgence of shrubs and an abundance of high-quality forage. Although fires are relatively rare, young moose do disperse (Peek 1974; Lynch 1976; Lynch and Morgantini 1984), increasing the probability of encountering and exploiting newly created habitats. Where forage quality and quantity are high, the twinning rate of moose is high, a rare phenomenon in large ungulates (Geist 1981*b*). Through dispersal and a high reproductive rate moose are able to exploit temporary, seral shrub communities (Geist 1971). As part of this opportunist strategy, the evidence presented here suggests that moose may also utilize a pheromonal priming system, similar to that of mice, to increase reproductive efficiency.

If scent urination acts to induce estrus, then males would only benefit if they associated with females at least periodically throughout the induction period to provide olfactory stimulation and be present during estrus. Duration of this proposed induction period is unknown but, given the difference in median dates of scent urination and copulation, would likely be 1–2 wk. In DNPP, there is evidence that some bulls are capable of defending cows over this time interval (D. G. Miquelle, V. Van Ballenberghe, and J. M. Peek, unpublished data), but only a small percentage of males are capable of such dominance, suggesting that scent urination would be advantageous to only a few males within a population. However, in a population of dispersed individuals (more characteristic of moose), more bulls would have opportunities to court solitary cows, so the benefits of scent urination would be extended to a greater percentage of the male population. Under these conditions, repeated encounters with females over the course of the rut would increase the probability that those males that scent urinated would receive a disproportionate share of copulations with the same females whose estrus they facilitated. Additionally, if scent urination makes bulls more attractive to cows, it would be advantageous for most bulls to engage in this behavior.

However, scent urination may be energetically costly for bulls. Scent urination is temporally correlated with and may be physiologically tied to hypophagia (Miquelle 1990). Cessation of feeding for approximately 2 wk contributes to dramatic weight losses during the rut (Schwartz et al. 1984, 1987). These costs may be offset for mature bulls that can defend cows from potential competitors, and who may gain an advantage by inducing ovulation before their body condition declines. Younger bulls, who may not experience complete appetite suppression (Miquelle 1990; but see Schwartz et al. 1984), may bypass scent urination in favor of feeding to increase body size, an important correlate of fighting ability and lifetime reproductive success (Clutton-Brock et al. 1982). Although young bulls may gain little from inducing ovulation because they are unable to defend cows from larger bulls, all bulls likely gain an advantage in acquiring the scent by making themselves more attractive to cows. Young bulls that do not scent urinate

may still attract cows by wallowing in pits of larger bulls. Employment of scent urination and scent marking appears to be an age- (or size-) dependent phenomenon in other cervids as well (Bowyer and Kitchen 1987; Miller et al. 1987).

Although moose are generally solitary, in DNPP they aggregate during the breeding season. Therefore, some aspects of scent urination observed here may not either be representative of moose in other environments or reflect conditions existent throughout their evolution. For instance, because cows are usually solitary elsewhere, competition for access to pits is unlikely. Observations from Isle Royale National Park (D. G. Miquelle, unpublished data) indicate that, while competition is rare, most of the behaviors observed in DNPP also occur in less gregarious populations.

Evolution of Priming Pheromones in Ungulates

If the evolution of priming pheromones is associated with the reproductive ecology of a species, it is likely to be most strongly developed in ungulate species that exist in populations of widely dispersed or unpredictably distributed individuals inhabiting seasonal environments. Strongly seasonal environments limit the birthing season (and therefore the breeding season) to a narrow window in time when the probability of offspring survival is greatest (Rutberg 1987; Festa-Bianchet 1988). In species that commonly aggregate during the breeding season, males will likely locate and remain with female groups or defend territories that are predictably located and easily found (Gosling 1986), so females are assured of the presence of a breeding male when they ovulate. Termination of seasonal anestrus in gregarious females, for whom the probability of associating with a male is high, is more likely to be spontaneous and physiologically set within a narrow window that coincides with the best birthing period.

For species like moose, in which females are often widely and unpredictably dispersed, the presence of a bull may not be guaranteed during behavioral estrus. Evidence of recurrent estrous cycles in some members of ungulate populations (Cheatum and Morton 1946; Plotka et al. 1977; Berger 1983; Pojar 1984) raises the possibility that either males were not present during estrus or there was a lack of synchrony in breeding behavior between the sexes. Under these conditions, a pheromonal priming system that induces ovulation may be an effective mechanism to ensure the presence of a bull and/or synchronize behavior between males and females. Spontaneous ovulation by a cow moose in the absence of a bull means a wait of a full estrous cycle, or about 25 d (Schwartz 1987), before breeding could occur. Such a postponement in breeding may be critically important in determining survival of offspring. A priming system that acts to ensure the presence of a bull during estrus and synchrony in breeding behavior would likely increase the probability of calf survival, thereby increasing the reproductive success of both the bull and cow.

Scent urination probably has several functions, and the importance of each likely varies among ungulate species. I suggest that scent urination may act to induce ovulation most commonly in ungulate species that are solitary (or live in small groups) or inhabit environments where forage is found in low densities or is sparsely distributed (e.g., rocky cliffs or continuous forests). When forage

resources exist in such a pattern, females (as a resource for males) will likely also be found at low densities or in an unpredictable pattern (Gosling 1986). If females cannot be assured of the presence of a male at estrus, they should wait for a signal from a male to terminate anestrus or risk waiting an entire estrous cycle for another breeding opportunity. Ovulation inducement has been postulated for solitary ungulate species other than moose (Miller et al., in press), although it has been proposed for some gregarious ungulates as well (Kennaugh et al. 1977; McComb 1987). The importance of priming pheromones may be most strikingly demonstrated by cow moose, whose strong reaction to bull urine suggests that priming may be a prerequisite for ovulation at the time most likely to ensure a successful reproductive effort.

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