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Significance of Scent-Marking by Roosevelt Elk

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cannibalism by very young mammals will likely be restricted to conspecific scavenging because their small body size and predatory skill limitations generally preclude intraspecific killing.

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SIGNIFICANCE OF SCENT-MARKING BY ROOSEVELT ELK

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The importance of scent-marking in mammalian communication has been well-documented (Eisenberg and Kleiman, 1972; Ewer, 1968; Gleason and Reynierse, 1969; Ralls, 1971). Leuthold (1977) noted that scent-marking among ungulates occurred in three general contexts: marking was performed most often by high-ranking individuals; marking typically was associated with agonistic interactions; and marking was most common near socially important locations in the home range. Scent-marking has been well-described for some ungulates, but much remains to be discovered about the situations that elicit scent-marking and the information it imparts. The purpose of this study was to describe and quantify three scent-marking behaviors

of Roosevelt elk (*Cervus elaphus roosevelti*) and to investigate the behavioral context in which scent-marking occurred.

Research was conducted on Gold Bluffs Beach, Prairie Creek Redwoods State Park, Humboldt Co., California (41°23'N, 124°06'W). This area is a narrow strip of coastal prairie separated from redwood (*Sequoia sempervirens*) forest by precipitous sandstone cliffs. The beach is intersected by many small creeks that are surrounded by stands of red alder (*Alnus rubra*). Further descriptions of the study area are provided by Harper et al. (1967), Franklin et al. (1975), and Bowyer (1981).

Elk were observed from 12 November 1972 to 28 November 1973; data were collected primarily during 311 h of intensive observation of elk behavior during the mating season (August–November 1973). Behavioral acts were recorded using focal-group sampling and an all-occurrences log (Altmann, 1974). Observations were made over distances of 5 to 100 m with the unaided eye or 7× binoculars from 0700–0200 h Pacific Standard Time. Most observations were made from a vehicle to minimize disturbance to elk. Data collection was terminated if elk exhibited alert or alarm postures resulting from our presence. The herd on Gold Bluffs Beach was composed of 4 master bulls (males that held harems during rut), 6 bachelor bulls, 3 yearling bulls, 19 cows (including 2 yearlings), and 7 calves.

Scent-marking was analyzed on an acts per active hour (A/AH) basis described in detail by Bowyer (1981). This procedure allowed comparisons between individuals in different sex and age classes that exhibited variations in activity patterns (Bowyer, 1981). Almost no social behavior occurred while elk were inactive (bedded).

The G-test of independence (Sokal and Rohlf, 1969) was used to compare rates of scent-marking behavior by different sex and age classes of elk. Expected values were generated by calculating the number of times a behavioral act would have occurred if sex and age classes of elk marked at the same rate.

Thrash-urinate.—During thrash-urination, bulls laid their ears back, unsheathed flaccid penises that palpated as large amounts of urine were excreted, raked their antlers back and forth, and used upward digging movements with the antlers that flung dirt and vegetation into the air. Thrashing and digging movements caused the penis to whip from side to side, spreading urine in a forward arc of about 2 m distance. Abdominal hair, the underside of the neck, and occasionally the sides of the face were saturated with urine. The surrounding vegetation and soil disturbed by antler thrashing also were soaked with urine.

Master bulls were not observed to urinate during rut without engaging in this behavior. Master bulls thrash-urinated for 1–368 s ($\bar{X} = 43$ s, $n = 177$), which was longer than for bachelor bulls ($\bar{X} = 16$ s, range = 5–24 s, $n = 14$). Master bulls pawed dirt and vegetation with a foreleg following 51 of 177 thrash-urinations, and bedded on top of the disturbed area 17 times. Bachelor bulls were not observed to paw or bed following 14 thrash-urinations. Yearling males, cows, and calves never were observed thrash-urinating. Master bulls thrash-urinated nearly five times more often than bachelor bulls. Significant ($G = 458.19$, $P < 0.001$, 4 *d.f.*) differences occurred in the overall rates at which different sex and age classes of elk thrash-urinated (Fig. 1).

Thrash-urination was linked with aggressive interactions between bulls. This act preceded 8% of 26 sparring matches (ritualized fights) between bachelor bulls, and accompanied both serious fights between bulls over possession of the harem. On 24 occasions master bulls thrash-urinated when bachelor bulls approached the harem; subordinates retreated in all but three cases. Bulls typically extended their muzzles into the air and sniffed as they approached one another, perhaps detecting the scent of a potential opponent. We detected a strong, foul odor from master bulls that increased in strength as rut progressed.

Rates of thrash-urination for the master bull that controlled the harem for most of rut (9-times) averaged 1.2 A/AH ($n = 47$) during 15–31 August, peaked at 1.6 A/AH ($n = 56$) during 1–15 September, and declined significantly ($G = 22.39$, $P < 0.001$, 2 *d.f.*) thereafter (16–31 September: 0.6 A/AH, $n = 21$; 1–15 October: 0.3 A/AH, $n = 28$) until he was defeated by a high-ranking bachelor bull (Blue Crescent). Rates of thrash-urination for Blue Crescent averaged 1.1 A/AH ($n = 39$) during 16–31 October and declined significantly ($G = 8.93$, $P < 0.005$, 1 *d.f.*) to 0.10 A/AH ($n = 1$) during 1–15 November as rutting activities subsided.

Wallow.—Master bulls initiated wallowing in marshy areas and rain-filled depressions by alternately thrash-urinating and pawing the ground with a forefoot. Bulls then lay in the wallow and rubbed their chest, the underside of the neck, and the sides of the face in the mud. Bulls often dug up mud with their antlers and then smeared it onto their backs. Wallowing was observed only during rut. Master bulls wallowed from 45–300 s ($\bar{X} = 214$ s, $n = 7$). Fresh mud on the pelage of two bachelor bulls suggested they had wallowed; a yearling bull wallowed for 23 s. Cows and calves never were observed wallowing. We found no evidence that wallows were reused by elk, but the large number of areas apparently suitable for wallows may have reduced the use of a particular site.

Overall differences in the rate at which wallowing occurred differed significantly ($G = 23.48$, $P < 0.001$,

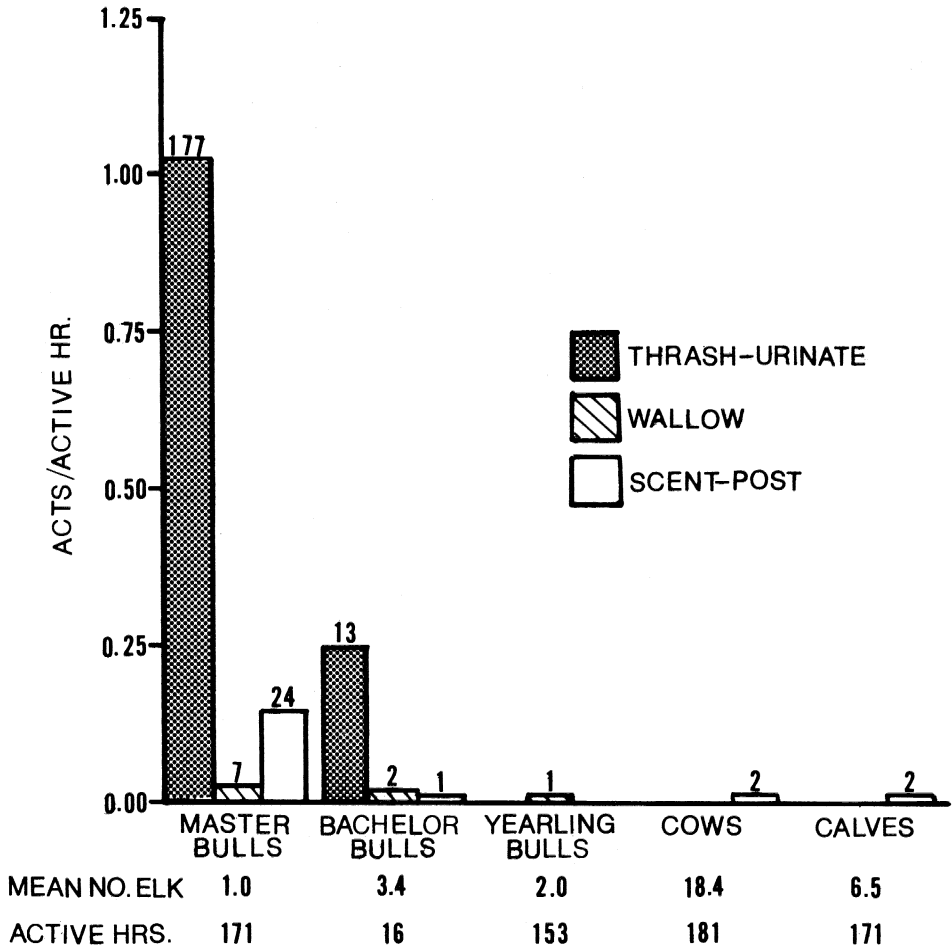


FIG. 1.—Rates (Acts/Active Hour) of scent-marking behaviors by different sex and age classes of Roosevelt elk on Gold Bluffs Beach, Prairie Redwoods State Park, Humboldt County, California, 1973. Sample sizes for scent-marking behaviors are given above bars. The mean number of elk observed per hour and the number of active hours for which they were observed are provided below each sex and age class.

4 *d.f.*) among sex and age classes. Rates of wallowing by master bulls exhibited a downward trend during rut (August: 0.07 A/AH, $n = 2$; September: 0.06 A/AH, $n = 4$; and October: 0.01 A/AH, $n = 1$). Bachelor bulls wallowed in September (0.46 A/AH, $n = 2$) and a yearling bull did so in October (0.01 A/AH, $n = 1$).

Scent-post.—Elk typically initiated scent-posting behavior by sniffing the trunk of a tree approximately 1 m above the ground. Bark was scraped from the tree with either the lower incisors or, for some bulls, with the brow tine of the antlers. The trunk was alternately licked and scraped, but the peeled bark was not eaten. Elk rubbed their foreheads, the sides of their faces including the preorbital glands, necks, and shoulders on the scrape. Elk laid their ears slightly backward and the tail occasionally was held erect during scent-posting. With the exception of scraping with the brow tine, behavior associated with scent-posting was similar for all sex and age classes of elk. Calves, however, were not observed to make their own scrapes, but twice marked trees immediately after a master bull completed scent-posting. These two instances were the only occasions in which we observed elk mark a tree that was scent-posted previously.

Scent-posting by master bulls lasted from 4–18 min ($\bar{X} = 8.5$, $n = 24$). The initiation of the behavior was not observed in the one instance where a bachelor bull scent-posted. Cows scent-posted for 1 min on one occasion and for 15 min on another. Calves marked for 28 s and 32 s in the two instances in which we

observed this behavior. Trees marked by elk included 28 red alders and one Douglas fir (*Pseudotsuga menziesii*).

Scent-posting occurred among all sex and age classes of elk (Fig. 1), but rates differed significantly ($G = 51.63, P < 0.001, 4 \text{ d.f.}$) with master bulls marking most often. Further, rates of scent-posting by age classes of bulls differed significantly ($G = 25.63, P < 0.001, 2 \text{ d.f.}$) with master bulls scent-marking most often.

Scent-posting was not associated with sexual or aggressive behaviors. During 42% of 24 scent-posting sequences by master bulls, cows were bedded within 10 m of males and exhibited no noticeable response to their activities. Similarly, when a yearling bull marked in late November, another yearling bull was bedded within 5 m and did not respond with aggressive or submissive postures. In the two instances cows were observed scent-posting, other females grazed and bedded nearby and did not respond to this marking behavior.

Unlike other scent-marking, scent-posting was not confined to rut, but occurred throughout the year (Franklin et al., 1975; Graf, 1955; Harper et al., 1967). Master bulls that were year-round residents on Gold Bluffs Beach scent posted at a rate (0.04 A/AH, $n = 2$) that was significantly lower ($G = 4.18, P = 0.05, 1 \text{ d.f.}$) than master bulls that occupied this area only during rut (0.19 A/AH, $n = 22$).

Potential functions of scent-marking.—Males of many species of ungulates urinate on themselves during rut (Coblentz, 1976). The vigorous nature of thrash-urination, the unsheathed penis, and the assumption that the fluid released was ejaculate led several authors to conclude that thrash-urination was a form of masturbation in *Cervus elaphus* (Altmann, 1952; Darling, 1937; Struhsaker, 1967). Others, however, have maintained that only urine was excreted during this behavior (Graf, 1955; Harper et al., 1967; McCullough, 1969). Elk semen is similar in appearance to the ejaculate of domestic cattle (W. C. Foote, Utah State Univ., pers. comm.) and is not clear like the fluid released during scent-marking. Moreover, the volume of fluid released far exceeded small amounts of semen obtained by electro-ejaculating elk (Foote, pers. comm.). Thus, it is likely that elk only urinate while thrashing during rut.

McCullough (1969) hypothesized that thrash-urination marked a bull elk with metabolic products contained in his urine. Elk master bulls undergo tremendous changes in physical condition during rut because they feed less and engage in more behavioral interactions than other sex and age classes (Bowyer, 1981; Flook, 1970; McCullough, 1969; Struhsaker, 1967). Thus, while in good condition, a bull metabolizes reserve body fat and sources of dietary energy, but as rutting activities bring about a decline in physical condition, he begins to metabolize muscle tissue (McCullough, 1969). By soaking himself and the surrounding environment with urine, a bull may advertise his physical condition to other males. Elk are sensitive to olfactory stimuli and should detect a shift in the metabolic products of a harem master's urine (McCullough, 1969). This behavior would be advantageous to a master bull and allow him to assert dominance and conserve energy by avoiding serious encounters with subordinate bulls while in prime condition. Thrash-urination may benefit other bulls inadvertently by permitting them to determine the most opportune time to challenge a master bull for possession of the harem. A master bull would be expected to discontinue thrash-urinating as his condition deteriorated. Although Roosevelt elk master bulls did not totally cease this behavior as they declined in condition, they significantly reduced the rate at which thrash-urination occurred. This decline in the rate at which master bulls thrash-urinated was not a result of an overall decrease in activity due to a loss of physical condition; the activity of master bulls increased throughout rut (Bowyer, 1981). Moreover, the association of thrash-urination with aggressive interactions between males suggests it functions as a dominance display. A bull that did not thrash-urinate would be advertising his weakness, and the absence of this display might precipitate serious challenges by other males.

Coblentz (1976) noted that dominant male goats (*Capra hircus*) had a stronger urine odor than subordinate males, whereas the urine of females possessed little scent. He reasoned that if urine served only to indicate the physical condition of a male, it should not smell different from the urine of females. Thus, Coblentz (1976) postulated that the strong odor of a male's urine might function to communicate his age and dominance, or possibly serve to mask the metabolites in a male's urine as he declined in condition.

The dominance rank of male *Cervus elaphus* shifts throughout rut in relation to changes in physical condition (Bowyer, 1976; Clutton-Brock et al., 1982; Flook, 1970; McCullough, 1969; Struhsaker, 1967). Thus, communication of dominance solely through strength of urine scent is unlikely because this odor increased as elk declined in condition and dominance. This strong odor, however, might initially mask the metabolites in a harem master's urine. This effect must be short-lived because master bulls faced serious challenges from bachelor bulls as their condition declined.

Coblentz (1976) further proposed that for male goats the primary significance of the odor derived from scent-marking was its influence on the timing of estrus. Convincing evidence exists that the odor of a male synchronizes estrus in female caprids (Coblentz, 1976). Kennaugh et al. (1977) implicated lipid production by sebaceous glands in the penis sheath of fallow deer (*Dama dama*) as being responsible for the strong

odor of a male's urine during rut. They also postulated that the function of this odor was related to the synchronization of estrus. Although thrash-urination in Roosevelt elk occurred largely in an aggressive context, the possible influence of this behavior in synchronizing estrous cycles in a harem offers one explanation for males continuing to thrash-urinate even when it advertises their declining physical condition.

McCullough (1969) suggested that wallowing performs a function similar to thrash-urination. Wallowing would allow the bull to saturate the parts of his body with urine that could not be reached by thrash-urinating. Roosevelt elk males confined wallowing to rut. This behavior may be similar in function to thrash-urination because bulls thrash-urinated prior to wallowing, suggesting a relationship in function between the two behaviors.

Potential functions of scent-posting.—Graf (1955, 1956) suggested that Roosevelt elk were territorial solely because they scent-posted. Franklin et al. (1975) also contended that Roosevelt elk female-calf herds were territorial. Ralls (1971) documented, however, that scent-marking does not necessarily indicate territoriality.

Territoriality for herds of female Roosevelt elk that is maintained through scent-marking rather than direct aggression is a concept that presents several problems. Franklin et al. (1975) claimed scent-posting was aggressive in nature. Indeed, similar marking of vegetation by other male cervids is often associated with aggression (Fuchs, 1977; Hirth, 1977; Kile and Marchinton, 1977; Kucera, 1978; Moore and Marchinton, 1974). Among deer of the genera *Odocoileus* (Hirth, 1977; Kile and Marchinton, 1977; Kucera, 1978; Moore and Marchinton, 1974) and *Axis* (Fuchs, 1977), however, scent-posting frequently is linked to antler-thrashing. Antler-thrashing among cervids clearly is a dominance display, and scent-marking in these species is assumed to have aggressive connotations. Antler-thrashing by Roosevelt elk was not observed in association with scent-posting, but instead was linked to urination (thrash-urinate). We observed no aggressive behavior associated with scent-posting by elk. The single instance of aggression following scent-posting reported by Franklin et al. (1975) occurred when a cow made threatening movements toward an observer. Elk on Gold Bluffs Beach were habituated to the presence of people (Bowyer, 1981) and often acted aggressively when approached too closely by humans.

Heavy use of the center portion of the home range and the exclusive occupation of this "core area" by elk on Gold Bluffs Beach led Franklin et al. (1975) to conclude the cow-calf herd was territorial. This "core area," however, was not defended by elk (Bowyer, 1981; Franklin et al., 1975), and Bowyer (1981) reported an intrusion by another herd into this central zone.

Finally, the hypothesis of territoriality for cow herds does not explain the function of scent-posting by males, or why they marked at a significantly higher rate than cows or calves. Eisenberg and Kleiman (1972) and Ewer (1968) suggested that one of the most common scents an animal contacts in its home range is its own. An animal's odor may serve to reassure, familiarize, and orient the animal as it moves through its home range (Ewer, 1968). Eisenberg and Kleiman (1972) further noted that exploration of a new environment often was associated with an increase in frequency of scent-marking. This would explain higher rates of scent-posting by master bulls that occupied the Gold Bluffs Beach only during rut than for bulls that occupied this area year-round.

The full explanation of complex scent-marking behaviors in *Cervus elaphus* will require further research especially with respect to the chemical analyses of the various physiological byproducts and secretions. We conclude, however, that scent-marking is not related to territoriality in Roosevelt elk.

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FATAL FALL BY BIGHORN LAMB

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Bighorn ewes (*Ovis canadensis*) inhabit precipitous terrain, which provides escape and protective habitat. Lambing and lamb rearing occur in this terrain. Mortality from loss of footing and falling is an ever present hazard to bighorn sheep as well as Rocky Mountain goats (*Oreamnos americanus*) (Holrout 1967; Geist, 1971; Wishart, 1978); however, few eyewitness accounts are reported in the literature.

During a study on reproductive success of bighorn sheep in Custer State Park, in the southern Black Hills of South Dakota, I observed an approximately 2-week-old lamb lose its footing and fall to its death.

On 10 July 1984 at approximately 1540 h (CDT), two ewes, each with a lamb, climbed the south rim of French Creek canyon, which is approximately 150 m deep at that point. The ewes and lambs were moving up a north-facing, exposed, granite cliff (Fig. 1). They had progressed about halfway up the cliff face when the fatal accident occurred. At the time, the lambs were moving about freely.

The lead ewe switched back at the end of a ledge to jump to a higher, opposite-running fracture (Fig. 1a). Her lamb started to follow, but then jumped back to the original ledge and moved back down this ledge to the second ewe and lamb. The second ewe and her lamb then made their way up the same ledge past this lamb. The second ewe turned at the end of the ledge and used the same route upward as the lead ewe. The second ewe's lamb followed immediately behind her. The lead ewe's lamb attempted to crowd along behind these two sheep. Although apparently not bumped, this lamb slipped backward at the top edge of