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Analysis of the *Flehmen* Display in American Bison (*Bison Bison*)

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ABSTRACT

A total of 873 *Flehmen* (lip curl) displays by bison (*Bison bison*) was recorded and statistically analyzed in relation to individual factors such as age and sex, and external factors such as wind speed, wind direction, temperature, humidity, and *Flehmen* stimulus to determine if differences between subgroups of individuals existed and if *Flehmen* was environmentally affected.

The mean lip curl display duration for all individuals was 8.4 seconds. Statistical tests of *Flehmen* duration means grouped by *Flehmen* stimuli showed a significant difference ($P < 0.05$). Lip curl duration means for males (8.3 sec.) and females (9.3 sec.), "maturity classes", all age-classes, cow age-classes, and bull age-classes were significantly different ($P < 0.05$). Because of a marked decrease of duration means for "prime" bulls, some relationship between *Flehmen* duration and sexual behavior of bulls was suggested. Windspeed, humidity, and temperature were determined to have little influence on lip curl duration. No significant correlation was found between lip curl direction and wind direction. Local variations of windspeed, wind direction, humidity, and temperature around the lip curling individual do not permit legitimate conclusions regarding their effect on *Flehmen* duration and direction.

INTRODUCTION

Flehmen, sometimes termed lip curling (Egerton 1962), grimacing (Cowan 1956, Harper et al. 1967, McCullough 1969, Gunderson 1976), "Flehmen-face" (Grubb 1974:466), and "holding mouth open posture" (Struhsaker 1967:96) is a facial expression of various perissodactyls, artiodactyls, and some carnivores after scenting some olfactory stimulus (Schneider 1930 from Fraser 1968, Dagg and Taub 1970, Eisenberg and Kleiman 1972, Verberne 1970,

1976). This activity (Fig. 1) has been observed and described in American bison (*Bison bison*) by several authors (McHugh 1958, Egerton 1962, Herrig and Haugen 1970, Shult 1972, Petersburg 1973, Lott 1974). Although not fully understood (Moulton 1967, Estes 1972, Shank 1972, Verberne 1976), *Flehmen* is believed to make the Jacobson's organ (vomeronasal organ) more effective (Knappe 1964 as cited by Gunderson 1976, Verberne 1970, Eisenberg and Kleiman 1972, Bützler 1974) and, in ungulates, aids in the detection of estrous females by males (McFarland and Clegg 1960, Fraser 1968, Estes 1972). Estes (1972) gives an excellent description of the mechanics of the lip curl display and functioning of the Jacobson's organ.

In bison, the lip curl display is usually of short duration and is exhibited toward one or more directions. It has been observed in all ages and both sexes of bison. The primary objective of this study was to determine if significant lip curl duration differences existed among various subgroups within the herd.

Secondary objectives were to determine if lip curl duration was environmentally affected and if a relationship existed between the lip curl direction and wind direction. Side to side head movements during *Flehmen* and descriptions of simultaneous inhaling give credence to the hypotheses that the display may be affected by external factors and a lip curling animal may orient its body or open mouth in relation to the wind direction.



FIGURE 1. Young bull exhibiting *Flehmen*.

MATERIALS AND METHODS

Bison were observed at Fort Niobrara National Wildlife Refuge, Valentine, Nebraska, 16 May - 23 August 1975. Of 873 lip curl displays recorded, 855 were of known direction and 695 were of known duration. The lip curls were statistically analyzed in relation to age and sex of the lip curling individual, and external factors such as wind speed, wind direction, temperature, humidity, and *Flehmen* stimulus.

Raising and extending the head is the immediate reaction of a bison to a *Flehmen* stimulus. An abrupt dropping of the head terminates the display; thus lip curl durations were accurately timed to the nearest second in the field with a stopwatch or the intervals were indicated on taped field notes. These intervals were then timed with a stopwatch during transcription of the tape.

Age and sex of the lip curling individual were recorded. Bison at Fort Niobrara during the summer of 1975 ranged in age from less than 1 year to 14 years. During each fall roundup, new calves are branded with the last digit of the year in which they were born (e.g. calves born in 1973 were branded with a "3"); thus, individuals could be accurately aged. Due to poor light, obscured view, or distance, 103 *Flehmen* durations were recorded for individuals whose precise age was unknown, but who were classified as calves, young or mature animals. The lip curling individual's identity and stimulus of the display were also recorded when known.

The herd was divided into five subgroups, "maturity classes" based on age, sex, and reported breeding activity of bison of similar age: mature bulls, 6-13 years; mature cows, 3-13 years; young bulls, 1-5 years; young cows, 1-2 years; and calves. Most bulls 1-5 years old are sexually mature (McHugh 1958, Fuller 1962, Halloran 1968), but due to their inability to successfully compete for cows, they usually do not breed until 6-7 years of age (McHugh 1958, Egerton 1962, Shackleton 1968, Shult 1968, Engelhard 1970, Herrig and Haugen 1970, Petersburg 1973, Lott 1974). Except for a few cases (Fuller 1962, Halloran 1968), cows do not breed until they are 2 years old (McHugh 1958, Haugen 1974, Lott 1974). During the summer fieldwork, 2-year-old cows at Fort Niobrara had not yet bred and thus were considered in a similar subgroup as the young bulls.

Flehmen stimuli at Fort Niobrara were divided into four categories: 1) investigation of a cow's vulva or genital region, 2) investigation of a cow as she urinated, 3) investigation of cow's urine on ground, and 4) sniffing ground, possibly cow's urine (Engelhard 1970, Herrig and Haugen 1970). Other less frequent causes included investigation of a cow or her urine prior to parturition, licking another individual (usually a cow licking her calf's perineal region as it suckled) and sniffing an individual, near urine, or genital region without contact. Most of the latter three instances involved young calves.

Flehmen directions were determined with a compass. Displays in two or more directions, no two of which differed more than 90°, were reduced to one in the following manner:

1. two directions: second direction was recorded unless it was of very short duration,

2. three directions: e.g. northeast (NE) to north (N) to NE, the direction recorded was NNE,

3. three directions: e.g. northwest (NW) to N to NE, the direction recorded was N.

All weather information was obtained from the U.S. Weather Service office at Valentine, Nebraska, 8 kilometers west of the refuge. Weather data at this station are recorded 45 minutes after each hour from 0500 to 1700 Central Standard Time (CST). After 1700 CST, readings are taken every 3 hours.

Lip curls that occurred between 15 minutes past the hour to 14 minutes past the following hour were analyzed in relation to weather data for that 60-minute interval (e.g. lip curls from 0815-0914 and weather readings taken at 0845 were analyzed together). The following modifications were employed when necessary:

1. Wind gusts were averaged with the base wind speed.

2. Wind speed, humidity, and temperatures were averaged for those lip curls occurring within the 3-hour spans from 1700 CST - 0500 CST.

Except where noted, one way analysis of variance and Duncan's Multiple Range tests were employed to determine significant differences among subgroup means. Calculations were made with an IBM 360/65 computer.

RESULTS

Both sexes and individuals of all ages, including calves, were observed lip curling. Males displayed *Flehmen* significantly more often than females, 631 and 171 respectively (Chi-square, $P < 0.05$), with the majority being performed by mature bulls. Females elicited *Flehmen* in mature individuals and in calves significantly more often than males (Chi-square, $P < 0.05$).

Thirty-seven calves less than 2 months old were observed lip curling. The youngest calf to lip curl was a 3-day-old female calf after it licked a 6-day-old calf's back. Of 23 displays exhibited by calves of known sex, 14 were by males and 9 by females. This difference was not statistically significant (Chi-square, $P > 0.05$), probably because of the small sample.

Lip Curl Duration Analysis

The mean duration for the 695 lip curls recorded in our study was 8.4 seconds (s). The shortest lip curl duration, 2 s, was recorded for a yearling bull, two calves, and a 9-year-old bull. The longest display, 30 s, was exhibited by an 8-year-old cow.

Statistical analysis of *Flehmen* duration means grouped by lip curl stimuli indicated a significant difference ($P < 0.05$). Subsequent analyses of age and sex class duration means were based on *Flehmen* stimuli numbers 1 and 2 for three reasons. 1) Duration means of the two stimuli were grouped together by the Duncan Multiple Range test at the .05 level, indicating they were similar. 2) Use of significantly different *Flehmen* stimuli in the analyses would result in false differences among duration means of sex and age classes. That is, differences among these subgroups' duration means may be a result of the stimulus rather than factors of sex or age. And, 3) these two stimuli were involved in 88% of the displays.

(*Flehmen*) displays caused by all stimuli categories were used in the analyses involving environmental factors since we felt that the effect of the stimulus would be minimal on the outcome.)

A significant difference was found among duration means of the 13 age classes, not including calves (F-test, $P < 0.05$) and between means of males (8.3 s, $N = 373$, $SD = 2.420$) and females (9.3 s, $N = 57$, $SD = 2.746$) (t-test, $P < 0.05$). Analysis of variance of 12 cow age-class duration means (Fig. 2) showed a significant difference (F-test, $P < 0.05$). Thirteen bull age-class duration means were also significantly different (F-test, $P < 0.05$), but were less variable (Fig. 2). Comparison of *Flehmen* duration means of the five maturity classes is shown in Table 1.

TABLE 1. Comparison of Means of the Five Bison "Maturity Classes"

Maturity Classes	N	Mean* (Seconds)	SD
Mature Bulls	340	8.3	2.29
Mature Cows	60	9.7	2.74
Young Bulls	109	9.0	2.68
Young Cows	7	7.4	1.27
Calves	30	5.4	2.43

*Significantly different, F-test, $P < 0.05$.

By use of Pearson Correlation Coefficients and multiple regression analysis, it was determined that wind speed ($r = 0.0333$, $P = 0.190$), humidity ($r = 0.0042$, $P = 0.456$), temperature ($r = -0.0373$, $P = 0.163$), and humidity/temperature ($P > 0.05$) had little influence on *Flehmen* duration of all individuals. A similar result was found when the mature bulls were considered separately; $r = 0.0170$, $P = 0.372$; $r = -0.0617$, $P = 0.117$; $r = -0.0811$, $P = 0.059$; $P > 0.05$, respectively.

Lip Curl Direction Analysis

No significant correlation was found between lip curl direction and wind direction (Pearson Product-Moment, $r = 0.0013$, $P = 0.489$).

DISCUSSION

Other researchers have observed both sexes and all ages of bison to lip curl. Engelhard (1970) and Petersburg (1973) commented that bulls lip curled more often than cows. In their ungulate studies, Dagg and Taub (1970), Estes (1972), and Shank (1972) noted a lower frequency of *Flehmen* by females. Our results support their observations. This would seem logical in view of a male's apparent need for the behavior to detect estrous females.

From previous studies it is unclear at what age calves begin exhibiting *Flehmen*. McHugh (1958) observed both male and female calves, 45 days or older, exhibiting *Flehmen* and, except for a 2-week-old female calf, Engelhard (1970) stated most calves lip curled near 3 months of age. During his studies at Wind

Cave National Park, Shult (1972:125) noted *Flehmen* by bison of both sexes and all ages "except calves during their first week". Egerton (1962) observed a 10-day-old calf performing a lip curl. Ages of most of the lip-curling calves reported by others were estimated. At Fort Niobrara, information about 16 known-age calves was recorded. Seventeen of 37 calf displays (46%) were by calves less than 3 weeks old. Reinhardt et al. (1978) noted that lip curling by Buran calves (*Bos indicus*) was primarily by males, with females being the principal partners, and inferred that calves less than one year old can differentiate odors. Our findings involving bison calves at Fort Niobrara agree with this. *Flehmen* behavior in the young calves illustrates that response to lip curl stimuli already is well-developed.

The mean lip curl durations for bison at Fort Niobrara were shorter than those previously reported for bison, and ungulates in general. Without reference to a specific ungulate, Dagg and Taub (1970:687) described *Flehmen* lasting "up to two minutes or more". Other researchers recorded lip curl displays with considerably shorter durations; elk (*Cervus canadensis*), "several seconds" (Struhsaker 1967:96); male feral goats (*Capra hircus*), 5-15 s (Shank 1972); domestic sheep (*Ovis aries*), goats (*Capra hircus*), cattle (*Bos taurus*), and horses (*Equus caballus*), 10-30 s (Alexander et al. 1974); wild goats (*Capra aegagrus*), "at least 10 seconds" (Schaller and Laurie 1974:119); red deer (*Cervus elaphus*), average about 1 minute (Bützler 1974). Five moose (*Alces alces*) lip curls timed by Geist (1963) during his study in British Columbia ranged from 10-25 s and had a mean of 17 s. Egerton (1962:78) stated adult bison lip curled "for at least 10 seconds, and occasionally for as long as 15 seconds". Shult (1972) observed lip curl durations of bison at Wind Cave National Park varying from 3 to 19 s and usually lasting 9-10 s for adult bulls. In his study, Petersburg (1973) reported that lip curl durations for mature bulls ranged from about 3 s to more than 15 s, averaging 8 to 10 s, while Herrig and Haugen (1970) recorded bull bison lip curls usually lasting for 10 s. Egerton (1962) also noted 7 lip curl displays by calves averaging 6.9 s. The average *Flehmen* duration for 46 calf lip curls at Fort Niobrara was 5.4 s (Table 1).

Among the bull age-classes, there was a marked decrease in the mean and variability of lip curl durations of the 7- and 8-year-old ("prime") bulls (Fig. 2). This, together with a higher frequency of bull lip curl displays, suggests a relationship between a bull's *Flehmen* behavior, sexual behavior, and his age. Hill et al. (1976) found that reproductive-age adult cats were more sensitive to catnip than either aged or immature animals. Similarly, prime bulls may have a more efficient Jacobson's organ, hence, have shorter lip curl durations.

Variation among cow age-class duration means may have resulted from the *Flehmen* stimuli they responded to. Cows do not try to detect estrous cows, and any strange odor may cause them to exhibit *Flehmen*. McHugh (1958) noted lip curling by cows after they had investigated a rotted skeleton, cows about to calve, new calves, and a torn scrotum of a bull. Other authors have recorded amniotic fluid, clumps of bison hair, blood, investigations of males, human urine, own urine, and placental membranes to cause lip curling, usually in cows (Egerton 1962, Herrig and Haugen 1970, Shult 1972, Petersburg 1973, Lott 1974).

The tendency for mature bulls to have shorter and less variable lip curl durations than cows and young bulls can be seen again in the data presented in Table 1. Except for young cows and calves, mature bulls have the shortest *Fleb-*

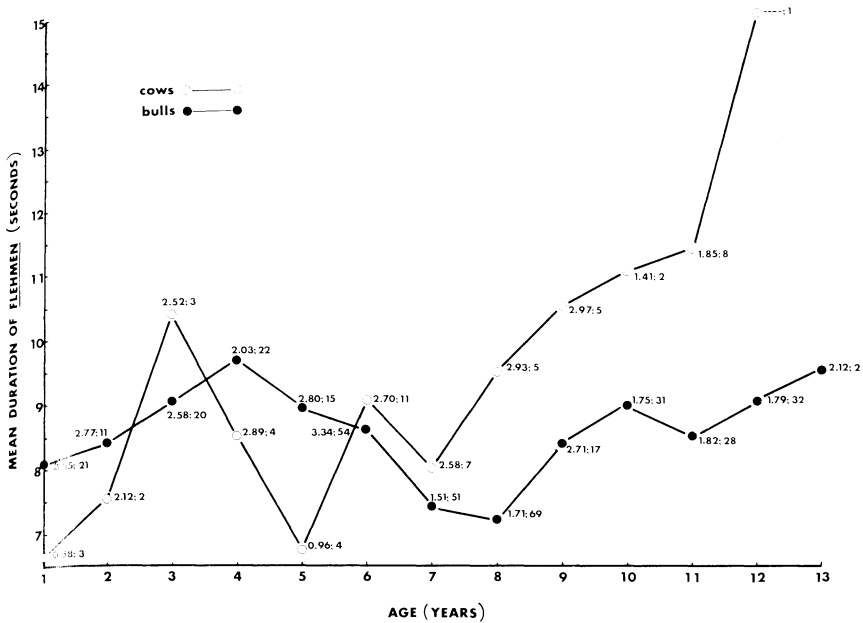


FIGURE 2. Comparison of cow and bull age-class duration means. Numbers by each point indicate standard deviation; sample size.

men duration mean, and except for young cows they also have the smallest standard deviation. This discrepancy may be a result of the young cows' small sample size. Also, calves react to many different odors and exhibit rather jerky, uncoordinated lip curl displays, generally of very short duration.

Petersburg (1973:82) noted that *Flehmen* in bison was accompanied by "audible forceful inhaling." Reinhardt et al. (1978:47) gave a description of *Flehmen* in Buran calves which is unclear in regard to the occurrence of inhaling; the calf "inhales and curls". Inhaling could be interpreted as preceding the lip curl or occurring simultaneously. Estes (1972) described how inhaling immediately prior to *Flehmen* would facilitate getting urine into the vomeronasal organ. This is similar to Bützler's (1974) suggestion that inhaling would permit better "tasting" of an odor by the Jacobson's organ and noted its occurrence during *Flehmen*.

Such inhaling would presumably be affected by wind speed, humidity, and temperature. However, Schneider (1932 as cited by Estes 1972) reported no breathing could be detected in a stallion as it lip curled. At Fort Niobrara, during our study and others (Gunderson, unpublished data), no breathing by the bison during *Flehmen* could be detected. Inhaling just before lip curling was not noted, but may have occurred. Estes (1972) suggested that in ungulates the most important function of the lip curl display was to close the external nares. This would explain our findings that external factors such as wind speed, humidity, and temperature had little, if any, effect on lip curl duration, and why we saw no breathing during the display.

In their description of *Flehmen* in domestic sheep, goats, cattle, and horses, Alexander et al. (1974) stated the male may move his head slowly from side to side. This is very similar to Geist's (1965) description of lip curling in mountain goats (*Oreamnos americanus*) and Bützler's (1974) description of red deer *Flehmen*. Bützler also mentioned that the head is sometimes thrown backwards, and speculated these movements presumably intensified the perception of the odor by taking in stronger air currents. McCullough (1969:82) stated that in elk, the lip curl display "is always directed into the wind, and the head is moved slowly in an arc on the windward side." During their study of bull bison behavior at Fort Niobrara, Herrig and Haugen (1970:253) noted, "It did not appear to matter if the bull was facing into the wind or away when displaying the lip curl." Their conclusion was based on direct observation rather than any type of analysis (Haugen, pers. comm.) but is supported by our finding that no significant correlation was found between lip curl direction and wind direction. Because the external nares are closed during *Flehmen* (Estes 1972), it would follow that wind direction would not affect lip curl direction. Since, however, local wind direction variations around lip curling individual bison and changes in wind direction during the 60-min period between readings at the weather station probably occurred, any conclusion about a lip curl direction-wind direction relationship is speculative.

Similar variations in other external factors such as humidity, temperature, and wind speed do not allow legitimate conclusions regarding their effect on lip curl duration. Our analyses illustrated differences of *Flehmen* duration means among bison age classes and males and females. Bull age-class duration means suggest some relationship to breeding behavior. Continued research in the areas of *Flehmen* duration and *Flehmen* direction may provide additional insight into this behavior and the functioning of the Jacobson's organ.

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