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The Influence of Rut and Environmental Factors on the Behaviour of Wood Bison

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Male and female wood bison (*Bison bison athabascae* Rhoads, 1897) were found to devote equivalent amounts of time to basic activities. Increased standing at the expense of feeding occurred during the rut and when the abundance of black flies (*Simuliidae*) was high. Weather had little effect on activity during the summer and fall study period. Results presented give some support to the suggestion that, in contrast to plains bison (*Bison bison bison* Linnaeus, 1758), there may be a trend away from a linear dominance hierarchy in male wood bison. Any such trend would be a function of small group size during the rut, which is suggested to be a function of the use of forest for feeding during the fall.

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1. INTRODUCTION

Free-ranging bison are found in four areas of northern Canada, Wood Buffalo National Park (WBNP), the Slave River Lowlands (SRL), Nahanni-Liard river drainages (NL), and the Mackenzie Bison Sanctuary (MBS). However, the SRL population declined from over 2,000 in 1970 to less than 400 in 1983 (Van Camp & Calef, 1987) and the WBNP population comprises a hybrid plains bison (*Bison bison bison* Linnaeus, 1758) — wood bison (*Bison bison athabascae* Rhoads, 1897) population, with a high prevalence of tuberculosis and brucellosis (Broughton, 1987). In constrast the MBS herd increased from 16 animals in 1963 to over 1,600 in 1987 (Gates & Larter, in press) and it now represents the major population of this sub-species (Wood bison recovery team, pers. comm.).

Although a number of detailed behavioural studies have been made on plains bison (McHugh, 1958; Herrig & Haugen, 1969; Lott, 1974; Maher

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& Byers, 1987), most research on northern Canadian bison remains of a more exploratory nature (Soper, 1941; Fuller, 1960). Even so, this work and the few more intensive studies do point to behavioural differences between bison in the boreal region and those of the plains, especially during the rut. The group size of mixed-sex herds can decline during the rut in northern bison, in contrast to the large aggregations seen in plains bison, and there may be an associated change in the male mating system (Calef & Van Camp, 1987).

The objective of this study is to provide novel baseline information on aspects of the behaviour of wood bison in a healthy expanding population. There is particular interest in comparing behaviour during the rut with that of plains bison and also investigating how environmental factors, including habitat, climate and biting flies, are related to wood bison group size and behaviour.

2. STUDY AREA AND ANIMALS

The Mackenzie Bison Sanctuary covers an area of over 6,200 km² on the west of the Great Slave Lake in the Northwest Territories, Canada (61° 30'N, 117° 00'W). It is located in the upper Mackenzie Section of the Boreal Forest Region (Rowe, 1972).

Three main open habitat types are associated with shallow lakebeds: wet sedge meadows occupy 2.8% of the sanctuary, savanna 2.3% and sparsely vegetated marls 9.5% (Mychasiw, 1987). Closed habitats comprise coniferous forest, including bog, (63.4%), mixed forest (19%) and willow (*Salix* sp.) — poplar (*Populus* sp.) woodland (5.7%). During summer (May to July) most bison use the savanna, while the coniferous forest is favoured in autumn (August to October) and wet sedge meadows are preferred in winter (November to April) (Larter & Gates, 1987).

Although wolves (*Canis lupus* Linnaeus, 1758) were present, no wolf-bison interactions were observed during the study and results are considered to reflect activities for a population little disturbed by predators.

3. METHODS

3.1. Activity Budgets

Activity data were collected using the instantaneous scan method (Altmann, 1974) and a ten minute interval. Bison activity was recorded for adult animals as either feeding, walking, standing, lying, sexual, aggression, or other. A total of 453 animal-hours of observation were conducted between June and October 1987, during the snow-free season. Herds were classified as either bull groups or mixed groups and herd size was noted.

The majority of watches were conducted in open habitats, particularly the favoured savanna, because of limited visibility in closed habitats. Statistical analyses of activity budgets were precluded because the scan interval was much less than

tthe duration of most activity bouts, resulting in non-independent data. The accuracy of activity data relies on large sample sizes.

A number of environmental parameters were quantified so that their effects on behaviour could be investigated. Wind speed was recorded as either light, less than approximately 20 km h^{-1}, or strong. Habitat used was classifed as one of the six categories listed above. Temperature was monitored in both open and closed habitats using thermograph recorders in Stevenson screens. Finally, the intensity of mosquitoes *(Culicidae)*, horse flies *(Tabanidae)* and black flies *(Simuliidae)* was noted on a five point scale from nil (0) to very bad (5) as judged by the discomfort to a researcher standing still for 30 s. Recordings were made regularly in open and closed habitats and when observing bison.

3.2. The Rut

In addition to scan sampling, 7.7 h of focal animal observations (Lehner, 1979) were made during the rut. These observations were on fully adult males in mixed herds. If more than one such animal was present, then the one believed most dominant from preliminary observations was chosen. During both scan and focal sampling, particular attention was taken of the outcome of attempted entrances into mixed herds by solitary bulls.

4. RESULTS

4.1. Activity Budgets

Male and female wood bison spent similar amounts of time in the activities recorded (Table 1). The effect of the rut on activity is investigated in Tables 2 and 3. Both males and females in mixed herds fed less, stood more and walked less during the rut; in addition males lay more. Males in bull groups also fed less during the rut, however least walking occured post-rut and the high level of lying during the rut was maintained post-rut.

During the rut bull group males fed more, walked more, layed down more and stood less than mixed group males (Table 4). Outside of the rut the increased proportion of time spent feeding was equivalent for

Table 1

Activity budgets for male and female wood bison expressed as percentage frequency of observations. [1] N — the number of bison activity observations made using 10 minute scan intervals.

	Feed	Walk	Stand	Lie	Sex	Aggression	Other	N[1]
Males	21.1	13.5	18.1	43.6	1.9	1.1	0.7	1171
Females	21.7	14.2	14.0	49.0	1.2	0	0	1545

males in either group type, but bull group males walked much less, stood more and lay more. Aggressive behaviour between males was only observed in mixed groups.

Table 2

Activity budgets for male and female wood bison during rut and post-rut periods, expressed as percentage frequency of observations; data for mixed herds only. [1] — see Table 1 for explanation.

	Feed	Walk	Stand	Lie	Sex	Aggression	N [1]
				Males			
Rut	12.9	10.0	24.7	46.2	4.0	2.2	550
Post-rut	33.7	34.7	1.9	28.9	0	1.0	104
				Females			
Rut	17.9	12.4	18.4	49.6	1.7	0	1055
Post-rut	29.8	18.0	4.5	47.8	0	0	490

Table 3

Activity budgets for male bison during rut and non-rut periods, expressed as percentage frequency of observations; data for bull groups only. [1] — see Table 1 for explanation.

	Feed	Walk	Stand	Lie	Aggression	Other	N [1]
Pre-rut	32.2	22.3	11.6	28.1	0	5.8	121
Rut	19.7	15.1	12.6	52.7	0	0	239
Post-rut	35.0	2.6	19.1	42.7	0	0.6	157

Table 4

Activity budgets for male bison during rut and non-rut periods, expressed as percentage frequency of observations; data for bull groups and mixed groups. [1] — see Table 1 for explanation.

	Feed	Walk	Stand	Lie	Sex	Aggression	Other	N[1]
				During the rut				
Bull group males	19.7	15.1	12.6	52.7	0	0	0	239
Mixed group males	12.9	10.0	24.7	46.2	4.0	2.2	0	550
				Outside the rut				
Bull group males	33.8	11.2	15.8	36.3	0	0	2.9	278
Mixed group males	33.7	34.6	1.9	28.9	0	1.0	0	104

Temperature had little effect on male or female bison behaviour, except perhaps for females to walk more on hotter days at the expense of lying (Table 5). Strong winds were associated with an increase in standing at the expense of feeding, walking and lying (Table 6). Moderate and heavy levels of black flies caused a large change in the rankings of activities, compared to when flies were absent (Table 7). In particular there was a decrease in feeding and an increase in standing when levels were heavy.

Small sample sizes for habitats other than those in the open hinder investigating the effects of habitat type on activity. In additon, the difficulty of observing bison in the forest biased the data set towards activities carried out on cutlines, (10 m wide linear paths cleared of trees), which are unlikely to be representative of total forest use. However, feeding results will be given as they illustrate the point that closed habitats were used for feeding and not just for travel. Bison spent 21.1% (n=2460) of their time in open habitats feeding, compared to 26.2% (n =256) in closed habitats.

Table 5

Activity budgets for male and female bison on hot days and other cooler days during July and August 1987, expressed as percentage frequency of observations. [1] — see Table 1 for explanation. [2] — see text for details.

	Feed	Walk	Stand	Lie	Sex	Aggression	Other	N[1]
				Hot days[2]				
Males	12.4	8.5	26.3	48.6	2.4	1.8	0	331
Females	17.9	16.0	18.8	45.5	1.7	0	0.2	655
				Other days				
Males	14.4	8.1	23.4	44.5	6.7	2.9	0	209
Females	19.5	6.3	17.3	54.9	1.7	0	0.2	410

Table 6

Activity budgets for bison on windy days and other days during July and August 1987, expressed as percentage frequency of observations. [1] — see Table 1 for explanation.

Feed	Walk	Stand	Lie	Sex	Aggression	Other	N[1]
			Light wind (0-20 km h^{-1})				
18.6	14.1	13.0	51.8	1.9	0.4	0.2	1189
			Strong wind (>20 km h^{-1})				
13.1	8.2	31.2	43.7	2.7	1.1	0	657

Table 7

Activity budgets of bison for the period July to September 1987 during four levels of black fly infestation, expressed as percentage frequency of observations. [1] — see Table 1 for explanation.

Activity	Black Fly Level			
	Absent	Light	Moderate	Heavy
Feeding	22.4	25.0	29.2	8.9
Walking	7.5	7.4	26.8	8.9
Standing	11.9	14.1	3.8	30.8
Lying	45.5	51.1	39.5	48.4
Sex	10.5	2.5	0	2.4
Aggression	2.2	0	0.1	1.1
N [1]	134	284	747	822

4.2. The Rut

The first observation of sexual behaviour was made on 21st July 1987 and the last such observation occurred on the 19th August 1987. These dates were taken as defining the rut and included all observations of lone males entering mixed herds accompanied by male-male aggressive behaviour.

A main feature of the rut, along with the occurrence of sexual and aggressive behaviour, was a change in group size. Data presented below

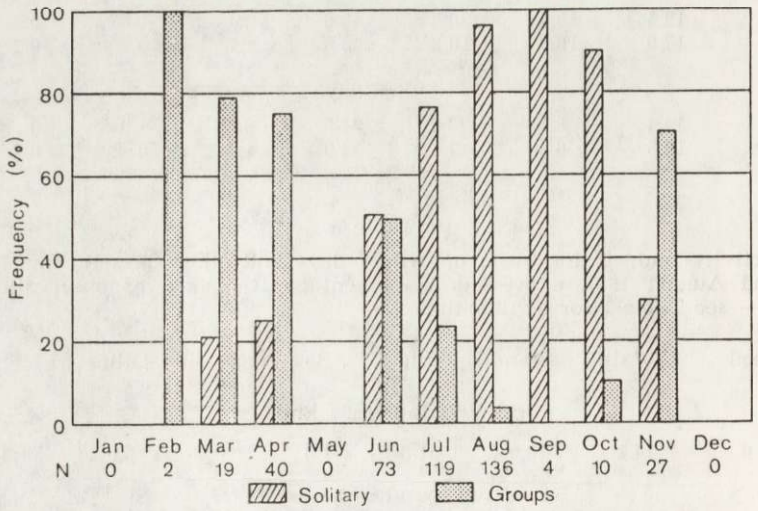

Fig. 1. The frequency of occurrence (%) of solitary males and bull groups, by month. N — number of observations.

are those from this study combined with additional observations made by one of us since June 1986 (Larter, 1988). Most bulls became solitary during the rut (Fig. 1); the mean bull group size of 1.1 ($n=188$, range 1-3) during the rut was significantly lower than the value of 2.4 ($n=243$, range 1-13) away from the rut (Mann-Whitney U test; $Z=9.72$, $p<0.001$). Mixed herds were more frequently of smaller size during the rut as compared to the June pre-rut sample (Fig. 2) ($\chi^2=15.25$, df$=3$, $p<0.01$). However, as with bull groups, this trend for small size appeared to extend throughout the autumn, and overall the mean group size of 30.7 (range 2-243) during the rut was not significantly different from the mean of 42.1 (range 2-255) for the non-rut period (Mann-Whitney U test; $Z=1.74$, $p=0.08$).

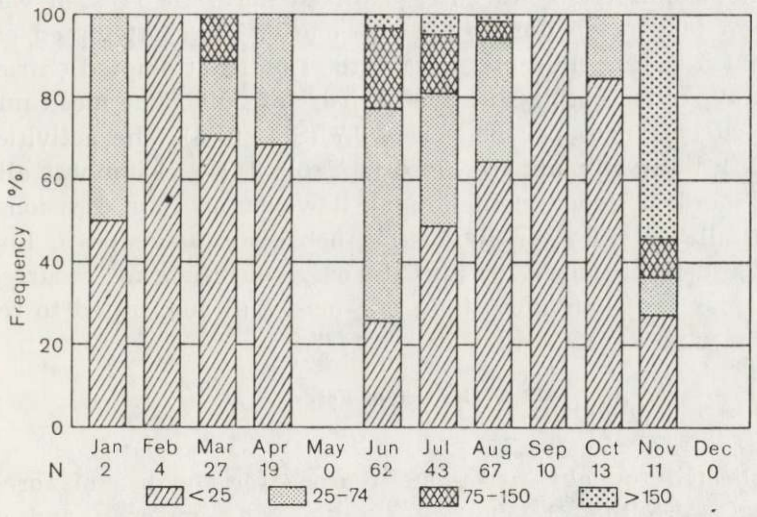

Fig. 2. The frequency of occurence (%) of four group sizes of mixed herd, by month. N — number of observations.

The 7.7 h of focal animal observations were spread across five groups. Group sizes ranged from 13 to 56 and the number of adult and subadult males present, excluding 2 year old spikehorns, ranged from two to nine. The ranking of activities of dominant males is not in agreement with the rankings given above for males in general during the rut. A dominant male is spending the majority of its time tending a female, while feeding was much reduced (Table 8). The following behaviours were seen and included under the term sex: blocking a female's movement, flehman, chin rest, mounting intention and copulation. Aggressive behaviour included stiff walking, pawing, wallowing, nod threat, broadside threat,

Table 8

Activity budget for dominant males (n=5) in mixed herds during the rut, from focal animal observations, expressed as percentage of time observed.

Feed	Walk	Stand	Lie	Sex	Aggression	Observation (min)
1.5	1.2	14.3	30.5	44.9	7.6	464

look threat, horning a tree, submission turn, light head butt, hard head butt, horning and massive fighting. The longest continuous fight lasted 1 min 58 s.

In all but a few cases aggression was between a dominant herd bull and a solitary bull trying to enter a mixed herd. Of 11 scan watches over 30 min long made during the rut, one or more attempted entries were observed during nine of them. A total of 14 attempted entries occurred, 12 by solitary bulls and two by pairs of bulls. The mean number of attempted entrances per hour was 0.7 (SD=0.68). The activities associated with these animals are listed in Table 9. No visitor was allowed to enter a herd as a dominant animal, however on four occasions animals were allowed in after submissive behaviour was shown. Encounters were usually resolved by threats only, but fighting occurred six times. On four occasions more than one herd bull cooperated to repulse a visitor.

4.3. The Use of Forest

Data collected to help investigate reasons for the use of forest by wood bison were the prevalence of biting flies in open and closed habitats and a comparison of temperatures between these two areas.

Table 9

Activities associated with the entrance of males into mixed herds during the 1987 rut. [1] — 12 entrances by solitary bulls and two by pairs of bulls.

Behaviour	Frequency
Number of male entrances seen [1]	14
Visitor kept out of herd	9
Visitor submissive & allowed into herd	4
Outcome uncertain	1
Encounter resolved by threats only	8
Encounter resolved by threats & fighting	6
Cooperation seen amongst herd bulls	4

No flies were seen during 14 observation periods during October. Between July and September tabanids and mosquitoes were rarely present above light levels (Table 10). Black flies, however, were often seen at light to heavy levels, with significantly ($p<0.01$) more in open habitats.

Table 10

The frequency of occurrence (%) of insects in open and closed habitats between July and September 1987. [1] — see text for details. [2] — number of observations made. [3] — observations not percentages tested.

	Severity Index [1]						
	Absent	Light	Moderate	Bad	Very bad	N[2]	Sig. [3]
			Black flies				
Open habitat	20.6	16.2	33.8	22.1	7.4	68	$\chi^2=23.72$, df=4, $p<0.01$
Closed habitat	42.1	33.3	19.3	0	5.3	57	
			Tabanids				
Open habitat	89.7	6.4	3.9	0	0	78	$\chi^2=2.87$, df=2, $p>0.05$
Closed habitat	89.7	10.3	0	0	0	58	
			Mosquitoes				
Open habitat	93.5	6.5	0	0	0	77	$\chi^2=3.45$, df=2, $p>0.05$
Closed habitat	86.2	10.3	0	3.5	0	58	

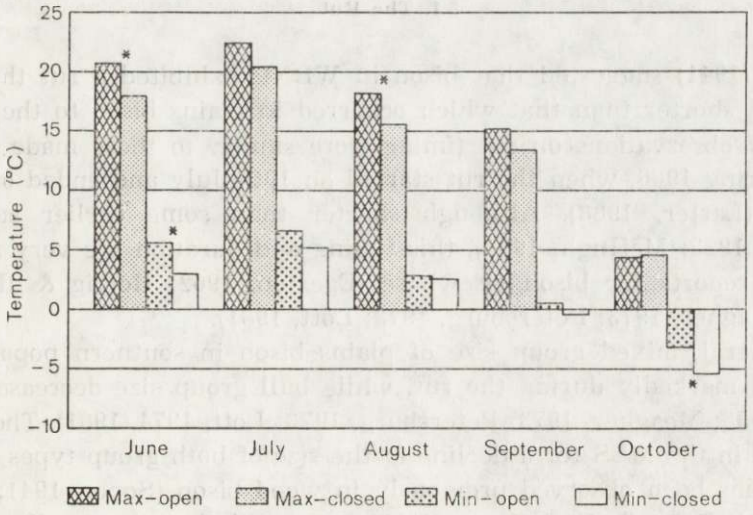

Fig. 3. Mean maximum and mean minimum temperatures recorded in open and closed habitats in the Mackenzie Bison Sanctuary during the 1987 study period. Significant differences (Student's t at least 2.06; p at least <0.05) between habitat types are marked with an asterix.

During summer and early fall mean maximum temperatures in open habitats tended to be higher than those recorded in closed habitats (Fig. 3). Likewise, mean minimum temperatures were also lower in the forest, significantly so during June and October (Student's t at least 2.06, p at least <0.05).

5. DISCUSSION

Male and female wood bison in the Mackenzie Bison Sanctuary appear to spend less time feeding and more time lying than American bison studied elsewhere (Hudson & Frank, 1987; Maher, pers. comm.) and less time lying than European bison, *Bison bonasus* Linnaeus, 1758 (Caboń-Raczyńska *et al.*, 1983). Some of the differences between study areas were probably caused by variation in the methods used for data collection, and the extent of nocturnal observations. For the American studies, the reduced percent of daylight feeding in the Mackenzie Bison Sanctuary can be partly attributed to the long hours of daylight at 61° North. Melton *et al.* (in prep.) discuss the possible significance of these activity results in the light of detailed feeding data and show that large males seem able to obtain sufficient food in the same time period as the smaller females, by being less selective.

5.1. The Rut

Soper (1941) suggested that bison in WBNP exhibited a rut that was later and shorter than that which occurred in plains bison to the south. Our 1987 observations on rut timing were similar to those made by one of us during 1986, when the rut started on 19th July and ended on 22nd August (Larter, 1988). Although shorter than some earlier accounts (Branch, 1929; McHugh, 1958), this timing and duration are very similar to most reports for bison elsewhere (Egerton, 1962; Herrig & Haugen, 1969; Meagher, 1973; Petersburg, 1973; Lott, 1981).

In general, mixed group size of plains bison in southern populations increases markedly during the rut, while bull group size decreases (McHugh, 1958; Meagher, 1973; Petersburg, 1973; Lott, 1974, 1981). The trend observed in the MBS for a decline in the size of both group types during the rut has been observed previously in wood bison (Soper, 1941; Egerton, 1962). Calef & Van Camp (1987) suggested that the smaller group size might represent a different mating system whereby a group of females was monopolised, however, they also thought that the poor condition of this population may have promoted small group size. We

have seen a dominant male leave a tended female to cross a small mixed herd to confront a visiting male, however this has also been reported for a clearly dominance ranked system of plains bison (Lott, 1974, 1981). A low density of known individuals precluded the monitoring of tenure ship of dominance by mixed herd bulls. The consistent success of herd bulls in repulsing intruders does give some support for the suggestion of a tendency towards seasonal harem formation in wood bison, but further study is needed to substantiate this interpretation.

The observed repertoires of sexual and aggressive behaviours are equivalent to those reported for plains bison (Lott, 1974, 1981). As noted by others, male-male interactions are usually resolved by threats (McHugh, 1958; Fuller, 1960, Meagher, 1973), but the proportion of actual fights in the MBS appears higher. This may again support the suggestion for a trend away from a linear dominance hierarchy.

The attempted movement of usually solitary bulls into mixed herds is a standard feature of the bison rut (Herrig & Haugen, 1969; Petersburg, 1973; Lott, 1974). The labelling of such animals as senile outcasts (Soper, 1941) is usually incorrect. Herrig & Haugen (1969) noted that both solitary visitors and herd bulls bred successfully, while Egerton (1962) saw lone bison successfully enter herds in WBNP, although it is unclear whether they were submissive or not.

5.2. Environmental Effects and the Use of Forest

The main effect of weather was for increased standing during summer an early fall when it was very windy, which may have been related to relieving the effects of biting flies. Others have also noted little effect of weather on bison activity (Herrig & Haugen, 1969; Van Den Brink, 1980), although the combination of heat and flies can cause animals to seek forest shade and reduce feeding (Soper, 1941; McHugh, 1958; Meagher, 1973; Van De Brink, 1980; Belovsky & Slade, 1986). Calef & Van Camp (1987) observed that an increase in group size of northern bison during a pre-rut period coincided with the use of open habitats and an increase in the abundance of biting flies. They suggested that increased wind in the open may be a causal factor, helping to alleviate the fly problem. In our study area flies were less prevalent in the forest.

Figure 4 summarises various factors possibly connected with the use of forest in the MBS. Open habitats are preferred from May to July and from November to Decembr, while most bison occur in forest from August to October (Larter & Gates, 1987). The rut starts as forest begins to be heavily used, however, forest utilization extends well past the end

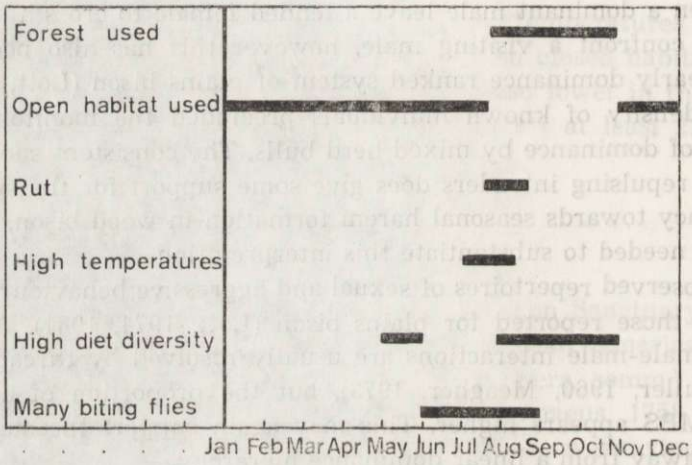

Fig. 4. The seasonal occurrence of factors possibly related to the use of forest by wood bison.

of the rut. Flies can be severe from June (pers. obs.) to September and they do cause a reduction in feeding and are more severe in the open. However, bison prefer open habitats during the first two months of the fly season and then stay in forest well after flies are reduced. Although forests offer a less extreme temperature regime in summer, their use only starts towards the end of the hottest period of the year.

These considerations suggest that neither the rut, nor climate, nor flies are the prime reason for forest use; as an alternative we suggest that food availability is the main causal factor. Forests in the MBS are used for feeding and not just for moving through to the open areas as suggested previously for American bison (Soper, 1941; McHugh, 1958; Meagher, 1973). Also an increase in diet diversity correlates well with forest use. Larter & Gates (1987) showed that sedges were the principal food during most of the year, apart from May, when shrubs showing a spring flush were favoured along with grasses, and the period August to October, when forest lichens formed a substantial part of the diet. Forest use seems related either to a preference for lichens at this time, or a decline in the acceptability of savanna herbs, or a combination of these factors. Krasińska *et al.* (1987) concluded that the main factor determining movement and habitat use of European bison within forests was the search for preferred forage areas.

The seasonal lowering of group size is probably a function of forest use. Others have noted that bison occur in smaller groups in closed habitats (Fuller, 1960; Shackelton, 1968; Van Vuren, 1983; Calef & Van Camp,

1987) and Krasińska *et al.* (1987) suggested that a group size of 20 may be optimal for bison in forests in both Europe and America. A trend for smaller groups in forest habitats is also common in other ungulates, where poor communication, resource patchiness and less predation can all be involved (Jarman, 1974). We conclude that the occurrence of small mixed herds during much of the rut is the result of resource use patterns and not a function of the rut itself. Likewise, in agreement with Lott's (1984) general model, any difference in the male mating system of wood bison as compared to plains bison would ultimately be a function of the environment.

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WPŁYW OKRESU ROZRODCZEGO I CZYNNIKÓW ŚRODOWISKOWYCH NA ZACHOWANIE BIZONA LEŚNEGO

Streszczenie

Stwierdzono, że zarówno samce jak i samice bizona leśnego *(Bison bison athabascae* Rhoads, 1897) poświęcają taką samą ilość czasu na podstawowe rodzaje aktywności (Tab. 1, 2). Tylko w okresie rozrodczym oraz czasie obfitości muszek *(Simuliidae)* zaobserwowano zmniejszenie czasu żerowania na korzyść nieruchomego stania w miejscu (Tab. 3, 4). Pogoda miała niewielki wpływ na aktywność w czasie lata i jesieni (Tab. 5, 6, 7).

Wydaje się, że u samców bizona leśnego występuje zaburzenie liniowej hierarchii dominacji (Tab. 8, 9, 10; Ryc. 1). Tendencja taka mogła by być wypadkową małej liczebności grup w czasie okresu rozrodczego. (Ryc. 2, 3), która z kolei wynika z żerowania w lesie w okresie jesieni (Tab. 10; Ryc. 4).