

BEHAVIORAL VARIATION IN BISON
(*BOS BISON BISON*) ON A
TALLGRASS PRAIRIE

By

ERIC J. MAICHAK

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University of Arkansas

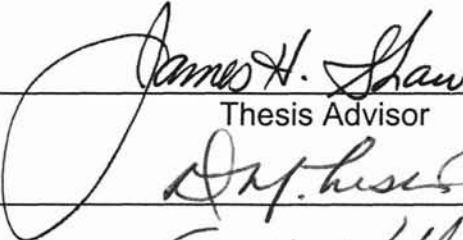
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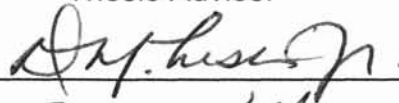
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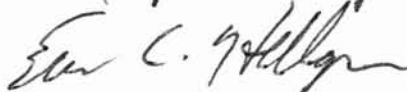
Thesis Approved:




Thesis Advisor



Dr. Phyllis N.



Evan C. Hollen



Dean of the Graduate College

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CHAPTER I

BEHAVIORAL VARIATION IN BISON (*BOS BISON BISON*) ON A TALLGRASS PRAIRIE

ABSTRACT

Behavioral studies of bison (*Bos bison bison*) have occurred primarily in northern and montane climates, accounting for seasonal, nutritional, and habitat effects on behavior. Behavioral differences between adults and calves during diurnal/nocturnal periods and effects of ambient temperature by season on bison behavior have not been well studied, particularly on southern tallgrass prairie. From May 2000 to May 2001, I observed adult and calf bison while they foraged, rested, and moved at the Tallgrass Prairie Preserve of The Nature Conservancy in north-central Oklahoma. My goals were to determine if 1) behavior differed between adults and calves among seasons and diurnal/nocturnal periods and 2) seasonal diurnal/nocturnal ambient temperature affected adult and calf behavior. Log-linear modeling indicated three-way interactions among bison age, season, and behavior, and among time period, season, and behavior. Chi-square tests indicated that individual diurnal behavior differed among seasons for calves and adults, between adults and calves within seasons, and between diurnal and nocturnal periods for adults. Univariable logistic models indicated that seasonal

ambient temperature (T_a) typically affected individual adult and calf behavior within diurnal/nocturnal periods, particularly during summer. Seasonal differences in behavior between adults and calves presumably were influenced by size and age-related thermoregulatory differences, seasonal and daily T_a , fluctuations in forage quality and quantity, and seasonal social interactions. Direct effects of T_a on seasonal variation in behavior suggested that bison are not equipped physiologically to tolerate T_a in summer. Therefore, they thermoregulate behaviorally to accommodate age and size-dependent thermoregulatory stress with respect to other weather variables and available forage.

Knowledge of daily and seasonal activity patterns is essential for evaluating foraging strategies and time budgets of herbivores (Cederlund et al. 1989), including bison (*B. b. bison*). Seasonal daily activity cycles of bison result from foraging time allocated to maximize energy intake (Belovsky and Slade 1986) or minimize time foraging (Bergman et al. 2001). Studies by Soper (1941) and McHugh (1958) showed that bison vary overall behavior among seasons and time periods. Studies of time budgets showed bison typically forage around sunrise, noon, and sunset (Caboń-Raczyńska et al. 1987), but this pattern varied in intensity among seasons, diurnal/nocturnal periods, and possibly with respect to forage quality (Rutley and Hudson 2001) and social status (Robitaille and Prescott 1993). Just prior to the rut, wood bison (*B. b. athabascae*) females with calves spent more time foraging than bulls or females without calves (Komers et

al. 1993). Higher dietary quality in calves than adults (Post et al. 2001) and age-related home-range differences found by Larter and Gates (1994) suggested bison have seasonal and age-related differences in behavior. Theoretically, time allocated to particular behavior should differ between bison of varying age based on differences in digestion (Demment and Van Soest 1985), surface area:volume, thermoregulation (Whittow 1971; Whittow 1973), and nutritional requirements (Robbins 1993). These requirements change in relation to seasonal forage quality and quantity (Coppedge et al. 1998), ambient temperature and other weather variable fluctuations (Belovsky and Slade 1986; Beier and McCullough 1990), or diurnal/nocturnal effects (Rutley and Hudson 2001).

Thermal stress from high or low T_a may have the strongest influence on behavior of large ruminants (Beier and McCullough 1990), potentially setting upper and lower limits on the time they devote to particular activities (Owen-Smith 1998). In laboratory studies, bison calves, like mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) (Parker and Robbins 1984), increase metabolic rate at $T_a < 0^\circ\text{C}$ and combat subsequent increased metabolic requirements by reducing overall daily activity (Christopherson and Hudson 1978). However, yearling bison under field conditions increase foraging and decrease resting from summer to winter (Rutley and Hudson 2001). Increased T_a (e.g., summer) increases metabolic rates of bison (Christopherson et al. 1979), mule deer, elk (Parker and Robbins 1984), moose (*Alces alces*) (Renecker and Hudson 1986), and feedlot steers (Lefcourt and Adams 1996). Presumably to combat thermoregulatory stress from high T_a and heat production from

rumination (Galbraith et al. 1998), bison reduce overall daily activity (Belovsky and Slade 1986), decrease daily foraging and intake (McHugh 1958; e.g., moose, Belovsky 1981; cattle, Morrison 1983; greater kudu [*Tragelaphus strepsiceros*] Owen-Smith 1998), and increase nocturnal foraging (Hudson and Frank 1987; Hein and Preston 1998).

Time budget, social interaction, nutritional, or thermoregulatory studies have failed to make direct seasonal and diurnal/nocturnal comparisons between adults and calves, occurred in montane or northern climates, or have compared adult and calf behavior in small enclosures (Soper 1941; McHugh 1958; Caboń-Raczyńska et al. 1987; Christopherson et al. 1979; Hudson and Frank 1987; Green 1992a, 1992b; Komers et al. 1993; Robitaille and Prescott 1993; Coppedge and Shaw 1998; Galbraith et al. 1998; Hein and Preston 1998; Bergman et al. 2001; Rutley and Hudson 2001). Plumb and Dodd (1993) concluded that bison do not graze at night, conflicting with observations of nocturnal grazing by bison (Hudson and Frank 1987; Hein and Preston 1998; Rutley and Hudson 2001). Ambient temperature effects on bison were related to thermoregulation in controlled lab settings, and behavioral accounts were anecdotal (Christopherson and Hudson 1978). Belovsky and Slade (1986) found that bison activity, not individual behavior, was influenced by summer T_a . Seasonal T_a significantly affects activity patterns of white-tailed deer (Beier and McCullough 1990) and may affect bison daily and seasonal behavior on tallgrass prairie. To my knowledge, no study has examined effects of seasonal T_a on adult and calf bison behavior during diurnal or nocturnal periods. I hypothesized that 1)

individual diurnal behavior would differ between adults and calves, within and among seasons; 2) individual adult behavior would differ between and within diurnal and nocturnal periods, within and among seasons; and 3) T_a would affect all adult and calf behavior during diurnal/nocturnal periods within individual season.

METHODS

Study Area

My study was conducted at The Nature Conservancy's 15,342-ha Tallgrass Prairie Preserve (TPP), located 25 km northwest of Pawhuska, Oklahoma, USA (36°50'N, 96°25'W). The area was characterized by C_4 tallgrasses, hilly topography, and rocky soils (Coppedge and Shaw 1998). Average daily temperatures in August and December were 27°C and 3°C, respectively. Precipitation usually occurred during spring and early summer thunderstorms; occasionally snowfall occurred from December to February, with mean annual precipitation of about 1,100 mm (Bourlier et al. 1979; National Oceanic and Atmospheric Administration 2000). One-third of TPP was burned annually (40% spring, 20% summer, 40% autumn) to provide a patch mosaic and reduce woody vegetation. Most burn patches were directly adjacent to one another, distributed from southwest to northeast across the middle of the 4,197-ha fenced bison enclosure, and were larger in 2000 ($N = 11$, $\bar{x} \pm SE = 154.2 \pm 43.5$ ha, max = 526.1 ha) than previous years (1993 – 1999; $N = 27$, $\bar{x} \pm SE = 102.5 \pm 15.9$ ha, max = 299.5 ha). The herd comprised about 900 adults (80% cows, 20% bulls, average age including yearlings = 5 yr and 3 yr, respectively) and 300 calves (< 1

yr old) in May 2000 and grew to 1,400 animals in May 2001 (R. J. Hamilton, The Nature Conservancy personal communication). Herd management included annual mid-October round-ups to cull bulls ≥ 6.5 yr, cows ≥ 13.5 yr, and 1/2 of bull calves, weigh animals, and give vaccinations for internal and external parasites. Supplemental feeding was restricted to several ad-lib mineral supplement stations (containing a general-purpose antibiotic to prevent anaplasmosis) distributed about 1 per 450 ha across the bison enclosure (Hamilton 1996).

Data Collection and Analysis

I collected > 1,300 scan-samples during 9 – 10 sampling periods per summer (24 Jun – 21 Sept) autumn (22 Sept – 20 Dec), winter (21 Dec – 20 Mar), and spring (21 Mar – 23 Jun). I did not sample during the mid-October round-up because it affected bison behavior and from 1 April 2001 to 1 May 2001 because bison cows and newborn calves were wary and unapproachable by foot. I randomly selected 1 of 3 main roads into the bison unit and selected the herd nearest to the entry point. I then randomly selected the first, second, or third bull, cow, or calf I encountered in a left-to-right scan sample of the herd and defined it as my focal animal. I followed the focal animal by foot and/or vehicle and defined bison within about 100 m of the focal animal as the herd. I scan-sampled (Altmann 1974) the herd for about 1 min from distances of 10 – 100 m using 10 x 50 binoculars every 30 min during periods of sun or moon light for ≤ 24 hr. I recorded specific behavior (foraging, movement, resting) for the first 20 adults (age \geq yearlings) and 20 calves (age < yearling) observed in the herd on a hand

held dictaphone and later transcribed the data. I defined foraging as grazing, cropping, or chewing (including mineral supplements); movement as any forward, reverse, or lateral movement, including playing, bounding, and stotting; and resting as standing (including tending), lying, or ruminating. During nocturnal periods (official sunset to official sunrise), I observed bison during moonlit hours from ≤ 100 m to increase accuracy of samples and omitted calves from data collection due to increased difficulty spotting them (Green 1986) behind larger bison or while lying down. Although I was unable to sample during moonless nights, I assumed moon phase had no influence on behavior (Collins et al. 1978).

Ambient temperature ($^{\circ}\text{C}$) was recorded by a Vaisala HMP35C temperature thermistor 1.5 m above ground level at the Foraker MESONET station located at the northeastern corner of the bison enclosure. I later obtained 30-min interval T_a data from the Oklahoma MESONET (Brock et al. 1995). During spring, no data were collected during 0100 hr and 0130 hr. Ambient temperature data (Table 1) were summarized from samples taken concurrently with behavior samples. Ambient temperature data (Fig. 1) reflected mean relative T_a at each 1-min sample every 30 min over 24 hr within individual season. Sample sizes for each interval ranged from 0 to 10. Lowest mean T_a occurred during late nocturnal and early diurnal periods and steadily increased throughout diurnal hours and steadily decreased throughout nocturnal hours (Fig. 1).

I assessed relationships of age, season, and behavior and time, season, and behavior with log-linear modeling (PROC CATMOD; SAS Institute Inc. 1989). Comparisons of behaviors of 1) calves diurnally among seasons, 2) adults

diurnally and nocturnally among seasons, 3) adults and calves during diurnal periods within individual season, and 4) adults between diurnal/nocturnal periods within individual seasons were evaluated with frequency distributions from Chi-square tests (PROC FREQ; SAS Institute Inc. 1989). I used individual bison response within each season and time period as the experimental unit for seasonal calf vs. adult comparisons and seasonal time comparisons. For behavioral comparisons among seasons and effects of ambient temperature on individual behavior within adults and calves, I set $\alpha \leq 0.05$. For tests of age and time differences, I corrected for multiple comparisons and set $\alpha \leq 0.001$.

To determine effect of T_a on individual behavior during diurnal or nocturnal periods and individual seasons, I obtained P -values and regression coefficients from maximum-likelihood Wald estimates in univariable logistic regression models (PROC LOGISTIC; SAS Institute Inc. 1989). Because results and interpretation of multivariable logistic models are confounded by dependent variables that are highly inter-correlated (Hosmer and Lemeshow 2000), I assumed individual behaviors were independent of one another and analyzed each separately by age, season, and time period. I categorized an “event” for foraging, movement, or resting as an observation of one adult or calf bison performing that behavior out of all observed in an individual 1-min sample, and a “non-event” as lack of observation of any bison performing that behavior. I transformed individual adult and calf events and non-events to percentages (number of animals performing a particular behavior out of all animals in a single 1-min sample, i.e., experimental unit) to summarize my data (Zhao et al. 2001)

and compared concurrent T_a and percent behavior for each individual 1-min sample in the logistic model. To determine the probability (%) of individual behavioral change with a T_a increase of 1°C , I used the odds ratio, a measure of association (Hosmer and Lemeshow 2000). That indicated how much more likely (odds ratio > 1) or unlikely (odds ratio < 1) an increase in foraging, movement, or resting was when compared with increasing T_a for an adult or calf within a season and diurnal/nocturnal period. For all logistic analyses, odds ratio of 1 implied no effect of T_a on the individual behavior; the farther an odds ratio was from 1, the greater the effect of T_a on that particular behavior. Because my sample sizes were < 400 , which reduced power of overall goodness-of-fit tests (Hosmer and Lemeshow 2000), I did not use goodness-of-fit tests to assess fit of individual models. I combined total number of 1-min observations for each individual behavior within a diurnal/nocturnal period within a season and used the percentage of all combined individual 1-min observations within a diurnal/nocturnal period within a season (number of animals performing a particular behavior out of all animals in a single diurnal and nocturnal period within a season) for presentation.

RESULTS

Seasonal, Age and Time Differences

I found a three-way interaction among age, season, and behavior (log-linear model: $\chi^2_6 = 348.06$, $P < 0.0001$; Fig. 2a, b) during diurnal periods. Diurnally, number of observations of calves foraging ($\chi^2_3 = 301.53$, $P < 0.0001$), moving ($\chi^2_3 = 155.28$, $P < 0.0001$), and resting ($\chi^2_3 = 856.34$, $P < 0.0001$) differed among

seasons (Fig. 2a). Within calves, foraging was lowest in spring and steadily increased through winter; resting was highest in spring and summer; movement was lowest among all behavior and stayed relatively constant among seasons. Diurnally, adult foraging was higher in spring than summer, but steadily increased from summer to winter; resting was highest in summer and spring; movement was lowest among all behavior and peaked in autumn.

I found a three-way interaction among time, season, and behavior (log-linear model: $\chi^2_6 = 531.46$, $P < 0.0001$; Fig. 2b, c). Within adults diurnally, foraging ($\chi^2_3 = 73.56$, $P < 0.0001$), moving ($\chi^2_3 = 97.00$, $P < 0.0001$), and resting ($\chi^2_3 = 574.68$, $P < 0.0001$) differed among seasons (Fig. 2b). Within adults nocturnally, foraging ($\chi^2_3 = 167.27$, $P < 0.0001$), moving ($\chi^2_3 = 92.56$, $P < 0.0001$), and resting ($\chi^2_3 = 504.79$, $P < 0.0001$) differed among seasons (Fig. 2c). Nocturnally, foraging was highest in summer, but resting was highest in all seasons except summer. Movement was lowest of all behavior, peaking in summer and decreasing through autumn and winter.

Frequency distributions of all behaviors differed between adults and calves within all seasons (Table 2). Overall, adults foraged more than calves in spring and summer and less in autumn and winter, moved more than calves in autumn and winter and less in spring and summer, and rested more than calves during autumn only (Fig. 2a, b). Therefore, I supported my first hypothesis that individual diurnal behavior would differ between adults and calves among and within seasons.

Frequency distributions of individual behaviors within adults differed between diurnal and nocturnal periods within each season (Table 3). To summarize, adults foraged more diurnally than nocturnally in autumn, winter, and spring but not summer, moved more diurnally all year, and rested more nocturnally in autumn, winter, and spring but not summer (Fig. 2b, c). Subsequently, I supported my second hypothesis that individual adult behavior would differ between diurnal and nocturnal periods among and within seasons.

Ambient Temperature Effects

Diurnal T_a typically affected adult behavior throughout the year (Table 4). During all seasons, adults were more likely to increase the proportion of time spent resting as T_a increased (Table 4). Effects of increasing diurnal T_a in summer were stronger than in all other seasons, decreasing time spent foraging and moving and increasing time spent resting. Other seasons showed similar, though weaker, effects of T_a on time spent in different behaviors. Movement was not affected by T_a in winter and spring (Table 4).

Ambient temperature typically affected nocturnal behavior of adults during all seasons (Table 5). Increasing T_a had stronger effects on nocturnal adult behavior in summer than in other seasons; however, time spent foraging and moving increased and resting decreased (Table 5), opposite to diurnal adult behavior in summer (Table 4). Effects of increasing T_a on nocturnal adult behavior in autumn and winter (Table 5) were not as strong as diurnal effects (Table 4). Time spent moving in winter decreased with increasing T_a . Nocturnal resting in spring

decreased while movement increased in response to increasing T_a ; foraging was unaffected (Table 5).

Ambient temperature typically affected all diurnal behaviors of calves in all seasons (Table 6), with effects strongest in summer. Likelihood of increasing diurnal resting with increasing T_a was higher than all other behavior among seasons. Movement in calves was least affected by increasing T_a by season, except in spring. Overall, effects of T_a on behavior of calves (Table 6) were very similar to adults (Table 4); exceptions occurred for foraging in spring and movement in winter and spring. Although seasonal diurnal and nocturnal T_a typically had an effect on individual behavior within calves and adults among seasons, lack of significance within adults, primarily for nocturnal behavior, prevented complete support for my third hypothesis that T_a would affect all behavior of adults and calves among seasons.

DISCUSSION

Age-related Variation in Bison Behavior by Season

Adult and calf behavior varied among seasons and diurnal/nocturnal time periods (Tables 2, 3; Fig. 2a, b). Observations of diurnal foraging by adults and calves were typically higher among all seasons than resting and movement which mirrors Caboń-Raczyńska et al.'s (1987) findings in European bison (*Bison b. bonasus*). Diurnal foraging of adults and calves tended to increase from spring to winter. Because quality of C_4 tallgrasses, primary bison forage (Coppedge et al. 1998), tends to decrease and become more homogeneous from spring to winter on tallgrass prairie (Waller et al. 1972), bison presumably must forage

more than rest to compensate for decreased forage quality (Robbins 1993) to maintain energetic balance (Demment and Van Soest 1985). Resting of adults and calves varied among seasons and was particularly high diurnally in spring and summer and low in autumn and winter; these findings concur with Rutley and Hudson's (2001) results on yearling bison in British Columbia. Thermoregulatory stress from increased T_a (Belovsky and Slade 1986; Owen-Smith 1998), ruminating heat production (Galbraith et al. 1998), relative humidity (Beier and McCullough 1990), and harassment from biting flies (McMillan 2000) and other ectoparasites (Byford et al. 1992) also may increase and decrease, respectively, time spent resting and foraging, particularly in summer. Adult and calf movement varied among seasons and occurred least of all behaviors. From spring to winter, diurnal calf movement decreases, probably in relation to decreasing forage quality and increasing forage homogeneity (Waller et al. 1972; Larter and Gates 1991), as calves wean, gain independence from their mothers, and become dependent on natural forage (Green 1992b).

In spring and summer, greater foraging by adults than calves probably results from increased nursing by newborn and young calves, and presumably increased foraging on recently burned patches (Coppedge and Shaw 1998) of nutritious forage (Waller et al. 1972) by lactating females (Caboń-Raczyńska et al. 1987; Komers et al. 1993) due to increased nutritional requirements of lactation (Robbins 1993). Because the study herd was extremely female-biased (5F:1M), my observed spring and summer adult foraging may be higher than in a 1F:1M population. Bison cows graze higher-quality forage than bulls on tallgrass prairie

range (Post et al. 2001). High-quality forage (e.g. low fiber, high N) typically has increased digestibility and decreased retention time, thereby allowing increased time foraging (Bergman et al. 2001) during lactation.

Greater resting by calves than adults in spring and summer is consistent with observations of bison calves by Robitaille and Prescott (1993). McHugh (1958) observed young calves playing in spring as did I, and in my study, playing was highly correlated with movement, which may explain why calves move more than adults in spring and summer (Larter and Gates 1994). Resting and playing (i.e., moving) are probably related to a more relaxed social environment from high numbers of seemingly protective adults (Green 1992a) because group size on tallgrass prairie tends to increase during spring (Schuler, unpublished data) and calves may be able to spend increased time resting or playing rather than maintaining vigilance or receiving supervision from mothers (Berger and Cunningham 1988) to prevent potential predation.

Diurnal movement of adults is least in spring, suggesting adults have access to ample nutritious forage during spring green-up at TPP (Coppedge and Shaw 1998). Most of the burn patches where I observed bison in spring 2000 and 2001 and summer 2000 were directly adjacent to one another and large enough to occupy several large (> 150 bison) herds. Bison may have increased foraging and resting (e.g., residence time) on large burn patches before depleting available forage and subsequently moving to new, adjacent patches (Krebs and Davies 1993). Increased diurnal adult movement in summer may be biased by the high numbers of cows and young bulls in the study herd. This may result from

displacement of cows by bulls performing tending behavior, particularly because cows often run from younger, sub-dominant bulls (Wolff 1998).

During autumn and winter, I observed calves foraging more and moving less than adults probably because calves were weaning during this period (McHugh 1958), and required more energy per unit body weight than adults to maintain basal metabolic rate (Demment and Van Soest 1985). Decreased daily T_a and exposure to solar radiation, additional wind effects (Beier and McCullough 1990), and increased surface area:volume (Whittow 1973) probably caused minor thermoregulatory stress (Christopherson et al. 1979). Had daily T_a in autumn or winter been as low as in Badlands National Park, South Dakota (Berger and Cunningham 1994), Yellowstone National Park, Wyoming (Meagher and Houston 1998), or Wood Buffalo National Park, Canada (Carbyn et al. 1993), adults and calves may have been more metabolically stressed (Christopherson et al. 1979) and may have decreased diurnal foraging and movement substantially to conserve energy. Statistical differences in resting between calves and adults in autumn and winter may have little biological significance and are potentially due to the power of the test to detect differences between populations when samples are very large (Steel et al. 1997).

Adult movement is highest in autumn and may result from decreased T_a and subsequent decreased thermoregulatory stress (Christopherson and Hudson 1979) after potential acclimation to summer T_a (Morrison 1983). Adults also may have been seeking increased nutritional quality and quantity of forage on burned patches from increased precipitation (Powell et al. 1986; Coppedge and Shaw

1998) after an extremely dry summer in 2000 (NOAA 2000). Observations of adult movement diurnally in winter possibly decrease from autumn because forage becomes less nutritious and more homogeneous, respectively (Waller et al. 1972). Therefore, bison move only to find more equally palatable forage when forage quantity is depleted within a particular area (Krebs and Davies 1993).

Daily Variation in Bison Behavior by Season

Several explanations exist for variation in the distribution of adult behaviors between diurnal and nocturnal periods and by season (Table 3; Fig. 2b, c). Foraging and movement occur primarily more diurnally than nocturnally, and vice-versa for resting, concurring with McHugh's (1958) finding that bison are generally diurnal with respect to overall activity. In summer, however, foraging occurs more nocturnally. These data support results showing bison in northern and montane environments increase nocturnal foraging during periods of increased T_a (Hudson and Frank 1987; Hein and Preston 1998), but conflict with Plumb and Dodd (1993) who concluded that bison do not forage nocturnally.

Adult bison in tallgrass prairie must tolerate extended periods of presumably extreme, thermoregulatory-stressing (Christopherson et al. 1979) diurnal T_a in summer and may not be well-equipped physiologically (Wittow 1973) to dissipate heat from elevated body temperatures diurnally. I observed bison sweating and panting during the afternoon in summer, which may alleviate some thermal stress if bison, like cattle (Taylor 1981), have a poorly developed countercurrent heat-dissipating mechanism. Because bison increase resting diurnally in summer, they may be using facultative hyperthermia (Taylor 1981), acclimating to high diurnal

T_a (Morrison 1983) by altering their daily activity cycle and dissipating stored heat nocturnally.

Ambient temperature is probably low enough from autumn through spring to allow thermoregulation (Christopherson et al. 1979) despite increased pelage thickness (Banfield 1974, from Reynolds et al. 1982), heat production from rumination (Galbraith et al. 1998), solar radiation, and effects of relative humidity (Beier and McCullough 1990). Consequently, adults forage diurnally and rest nocturnally. Insect harassment also is more common in summer than all other seasons (McMillan et al. 2000), potentially more so diurnally than nocturnally (Melton et al. 1989), which also may contribute to increased nocturnal foraging in summer. In summer, however, I often noticed adults continuing to swing their heads and tails to deter marauding insects throughout the night.

Adults decreasing movement nocturnally from summer to winter and then increasing movement in spring suggests that adults are thermogenically stressed during colder T_a (Christopherson et al. 1979) without additional heat gain from solar radiation (Walsberg 1983). However, higher nocturnal adult movement in summer than other seasons may be related to increased social interactions (McHugh 1958) caused by rut; i.e., displacement of cows by young bulls (Wolff 1998) attempting to copulate (Reynolds et al. 1982). Nocturnal movement was lowest in winter and probably due to nutritional homogeneity of forage (Waller 1972) and potential increased thermoregulatory stress from cold T_a (Christopherson et al. 1979) resulting in decreased activity (Christopherson and

Hudson 1978) or lying to reduce surface area:volume (Whittow 1973) to conserve energy.

Temperature-related Variation in Bison Behavior

Overall, I found T_a effects on individual behavior strongest in summer for both adults and calves. Increased solar radiation, relative humidity (Beier and McCullough 1990), heat production from rumination (Galbraith et al. 1998), dark pelage and skin color (Meagher 1979), and/or insect harassment (McMillan et al. 2000) may synergistically increase summer T_a effects more than other seasons. Both adults and calves thermoregulate behaviorally by decreasing diurnal foraging and movement and increasing resting (Hudson and Frank 1987; Lefcourt and Adams 1996; Hein and Preston 1998; Owen-Smith 1998). During autumn, seasonal and daily mean T_a were similar to winter temperatures and were probably less stressful on thermoregulation (Christopherson et al. 1979), allowing adults and calves to increase diurnal activity in autumn and winter (Fig. 2a, b) after becoming acclimated to higher summer T_a (Morrison 1983). Had daily T_a in autumn or winter been as low as in northern and montane areas (Carbyn et al. 1993; Berger and Cunningham 1994; Meagher and Houston 1998), adults and calves may have been more metabolically stressed (Christopherson et al. 1979). This could have resulted in stronger, more significant effects of T_a on adult and calf behavior.

In winter, bison, like moose, mule deer, and elk, drastically increase metabolic rate and become heat-stressed at T_a beyond 10°C (Christopherson et al. 1979; Parker and Robbins 1984; Renecker and Hudson 1986), presumably explaining

small decreases in foraging and increases resting diurnally in autumn and winter. Spring T_a are higher than autumn and winter temperatures, which may increase heat stress (Christopherson et al. 1979) on adults and cause decreased foraging. For adults in winter and spring, movement is not affected by increasing T_a and may result from skewed observational data; i.e., too few numbers of observed movement events and too many observed non-events to detect significance in the logistic model. Similarly, skewed observations of calf foraging may have resulted in no effect of spring T_a (Hosmer and Lemeshow 2000). For calves, decreasing movement and increasing resting as spring T_a increases probably results from calves decreasing movement as mothers typically decreased foraging and increased resting throughout diurnal periods. However, increasing spring T_a may cause thermoregulatory stress in calves due to their large surface area/volume ratio (Whittow 1973) and high metabolism (Whittow 1971).

Nocturnally, individual adult behavior was most affected by T_a in summer, excluding movement in winter and spring. This may result from decreased additive solar radiation and relative humidity effects (Beier and McCullough 1990). Increased foraging and movement and decreased resting probably occurred during early nocturnal periods in all seasons (Belovsky and Slade 1986; Hudson and Frank 1987; Hein and Preston 1998; Rutley and Hudson 2001; Maichak, unpublished data) to increase nutritional quality of forage intake (Kazmaier, personal communication) or thermoregulate behaviorally. Because bison core body temperature increases with rumination (Galbraith et al. 1998) and T_a at TPP decreases throughout nocturnal hours until sunrise (Fig. 1), bison

may decrease heat stress and thermoregulatory costs (Christopherson et al. 1979) by feeding and moving to maintain increased body surface exposure (Whittow 1973) and ruminating (i.e., resting) as nocturnal T_a decreases.

In winter and spring, increased T_a had strong effects on movement. I typically observed adults foraging from about 0200 hr to 0400 hr, similar to Rutley and Hudson's (2001) findings in yearling bison, but rarely saw bison move until late nocturnal (0500 hr to 0600 hr) and early diurnal periods (0700 hr to 0900 hr), when they would move to an entirely new area to commence feeding. Forage biomass is reduced throughout the time bison spend on a particular area (i.e., mid-diurnal to early diurnal periods), causing bison to move to a new area after forage biomass is reduced below a certain level (Krebs and Davies 1993), which may coincide with late nocturnal times. In spring, increasing nocturnal movement with T_a may result from increased social interactions and rut behavior during early nocturnal periods (McHugh 1958; Wolff 1998) or from adults, particularly lactating females, seeking recently burned patches (Coppedge and Shaw 1998) of highly nutritious forage (Waller et al. 1972).

Overall, behavior of bison varies among seasons within and between adults and calves suggesting that various physiologic, environmental, and social interactions influence behavior. Ambient temperature typically has a significant influence on adults and calves diurnally and nocturnally over the entire year but is strongest in summer. Failure to detect significance during various seasons and time periods suggests more in-depth studies of bison behavior should occur. Future studies of direct effects of T_a and synergistic interactions with relative

humidity, wind, and solar radiation on bison behaviors and physiological adaptations and responses also are warranted.

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APPENDIX A--TABLES

Table 1. Mean, maximum, and minimum ambient temperature (°C) during summer, autumn, winter, and spring at Tallgrass Prairie Preserve^a, Osage County, Oklahoma.

Period/ Season	Mean	SE	Max	Min
Diurnal				
Summer ^b	29.3	0.3	37.1	16.2
Autumn	7.2	0.6	27.7	-8.2
Winter	4.4	0.5	18.0	-15.1
Spring	21.8	0.3	29.6	7.4
Nocturnal				
Summer	24.7	0.3	31.0	20.2
Autumn	3.7	0.7	23.1	-5.5
Winter	2.0	0.4	12.6	-14.6
Spring	16.6	0.6	25.6	4.6

^a Results derived from temperatures taken with concurrent behavior samples

^b Summer = 24 Jun – 21 Sept; Autumn = 22 Sep – 20 Dec; Winter = 21 Dec – 20 Mar; Spring = 21 Mar – 23 Jun

Table 2. Frequency distribution results for seasonal comparisons of adult/calf bison behavior at Tallgrass Prairie Preserve, Osage County, Oklahoma.

Behavior/ Season	n	χ^2 (df=1)	P†
Foraging			
Summer	3135	208.77	<0.0001
Autumn	3439	172.85	<0.0001
Winter	3203	156.94	<0.0001
Spring	3049	1116.44	<0.0001
Movement			
Summer	905	17.27	<0.0001
Autumn	742	58.31	<0.0001
Winter	365	52.93	<0.0001
Spring	778	16.70	<0.0001
Resting			
Summer	3582	178.67	<0.0001
Autumn	1455	68.20	<0.0001
Winter	1320	64.59	<0.0001
Spring	3442	41.07	<0.0001

† significance set at $P \leq 0.001$; all comparisons significantly different

Table 3. Frequency distribution results for seasonal comparisons of diurnal/nocturnal behavior of adult bison at Tallgrass Prairie Preserve, Osage County, Oklahoma.

Behavior/ Season	n	χ^2 (df=1)	P†
Foraging			
Summer	2784	483.33	<0.0001
Autumn	2984	503.71	<0.0001
Winter	2917	339.40	<0.0001
Spring	2931	1314.69	<0.0001
Movement			
Summer	682	177.57	<0.0001
Autumn	626	167.69	<0.0001
Winter	298	142.40	<0.0001
Spring	522	262.26	<0.0001
Resting			
Summer	2911	743.33	<0.0001
Autumn	2311	126.65	<0.0001
Winter	2227	169.84	<0.0001
Spring	2576	598.82	<0.0001

† significance set at $P \leq 0.001$; all comparisons significantly different

Table 4. Logistic regression models* for the effect of diurnal ambient temperature by season on adult bison behavior at Tallgrass Prairie Preserve, Osage County, Oklahoma.

Season/ Behavior	Coefficient†	SE	Odds Ratio‡	95 % C.I.	P§
Summer (n = 224)					
Foraging	-0.16	0.01	0.86	0.84-0.87	<0.0001
Movement	-0.07	0.01	0.93	0.92-0.95	<0.0001
Resting	0.20	0.01	1.22	1.20-1.24	<0.0001
Autumn (n = 185)					
Foraging	-0.02	0.00	0.98	0.97-0.99	<0.0001
Movement	-0.03	0.01	0.97	0.95-0.98	<0.0001
Resting	0.04	0.00	1.04	1.03-1.05	<0.0001
Winter (n = 188)					
Foraging	-0.05	0.01	0.96	0.95-0.97	<0.0001
Movement	0.02	0.01	1.02	1.00-1.04	0.08
Resting	0.05	0.01	1.05	1.04-1.05	<0.0001
Spring (n = 278)					
Foraging	-0.06	0.01	0.94	0.93-0.96	<0.0001
Movement	-0.01	0.01	0.99	0.97-1.01	0.31
Resting	0.06	0.01	1.07	1.05-1.07	<0.0001

* df for all tests = 1

† Regression coefficient (SE) in the logistic model

‡ Odds ratio indicates probability that bison increase behavior as ambient temperature increases

§ Wald's test; significance set at $P \leq 0.05$

Table 5. Logistic regression models* for the effect of nocturnal ambient temperature by season on adult bison behavior at Tallgrass Prairie Preserve, Osage County, Oklahoma.

Season/ Behavior	Coefficient†	SE	Odds Ratio‡	95 % CI	P§
Summer (n = 82)					
Foraging	0.15	0.02	1.16	1.11-1.21	<0.0001
Movement	0.15	0.03	1.17	1.09-1.25	<0.0001
Resting	-0.24	0.03	0.78	0.75-0.82	<0.0001
Autumn (n = 122)					
Foraging	0.02	0.02	1.02	1.01-1.03	<0.0001
Movement	-0.01	0.01	0.98	0.96-1.01	0.14
Resting	-0.02	0.01	0.98	0.97-0.99	0.002
Winter (n = 139)					
Foraging	0.01	0.01	1.01	0.99-1.03	0.31
Movement	-0.11	0.03	0.90	0.85-0.95	0.0003
Resting	0.00	0.01	1.00	0.99-1.02	0.79
Spring (n = 77)					
Foraging	0.00	0.01	1.01	0.99-1.04	0.42
Movement	0.17	0.02	1.63	1.45-1.85	<0.0001
Resting	-0.05	0.01	0.96	0.93-0.98	0.0007

* df for all tests = 1

† Regression coefficient (SE) in the logistic model

‡ Odds ratio indicates probability that bison increase behavior as ambient temperature increases

§ Wald's test; significance set at $P \leq 0.05$

Table 6. Logistic regression models* for the effect of diurnal ambient temperature by season on calf bison behavior at Tallgrass Prairie Preserve, Osage County, Oklahoma.

Season/ Behavior	Coefficient†	SE	Odds Ratio‡	95 % CI	P§
Summer (n = 232)					
Foraging	-0.15	0.01	0.86	0.85-0.88	<0.0001
Movement	-0.08	0.01	0.92	0.90-0.94	<0.0001
Resting	0.20	0.01	1.22	1.20-1.25	<0.0001
Autumn (n = 181)					
Foraging	-0.03	0.01	0.97	0.96-0.98	<0.0001
Movement	-0.02	0.01	0.98	0.97-1.00	0.03
Resting	0.05	0.01	1.05	1.04-1.06	<0.0001
Winter (n = 145)					
Foraging	-0.05	0.01	0.96	0.94-0.97	<0.0001
Movement	-0.04	0.01	0.96	0.93-0.98	0.002
Resting	0.07	0.01	1.07	1.05-1.09	<0.0001
Spring (n = 189)					
Foraging	-0.01	0.01	0.99	0.97-1.02	0.54
Movement	-0.13	0.02	0.88	0.85-0.91	<0.0001
Resting	0.08	0.01	1.08	1.06-1.10	<0.0001

* df for all tests = 1

† Regression coefficient (SE) in the logistic model

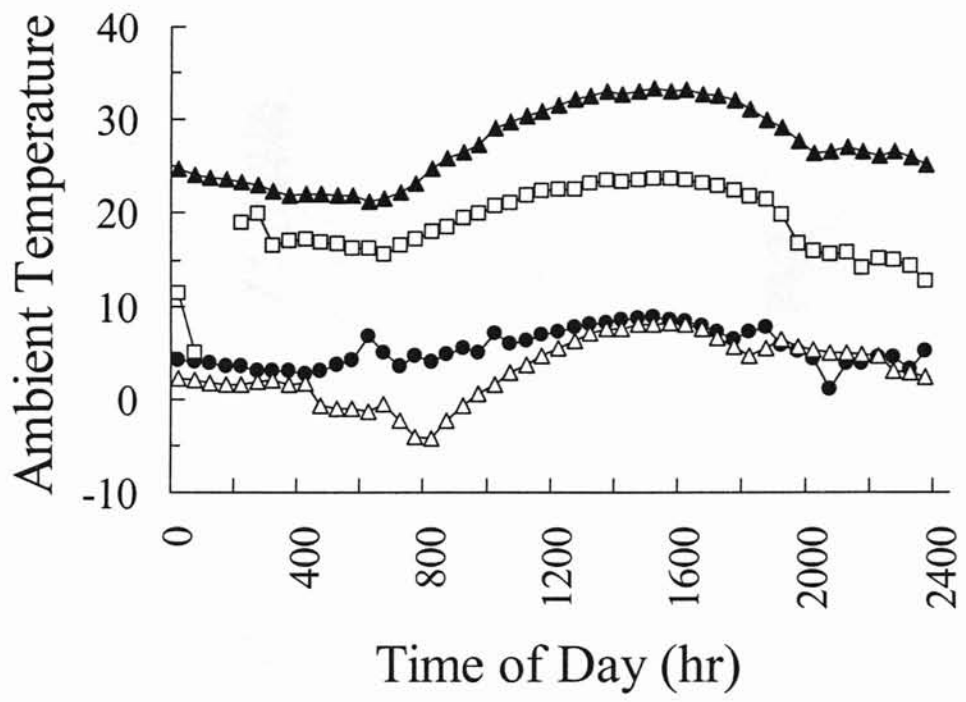
‡ Odds ratio indicates probability that bison increase behavior as ambient temperature increases

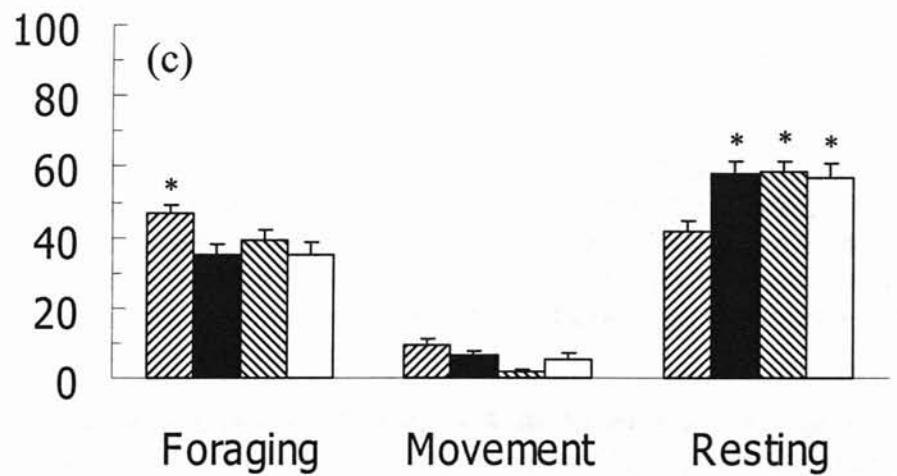
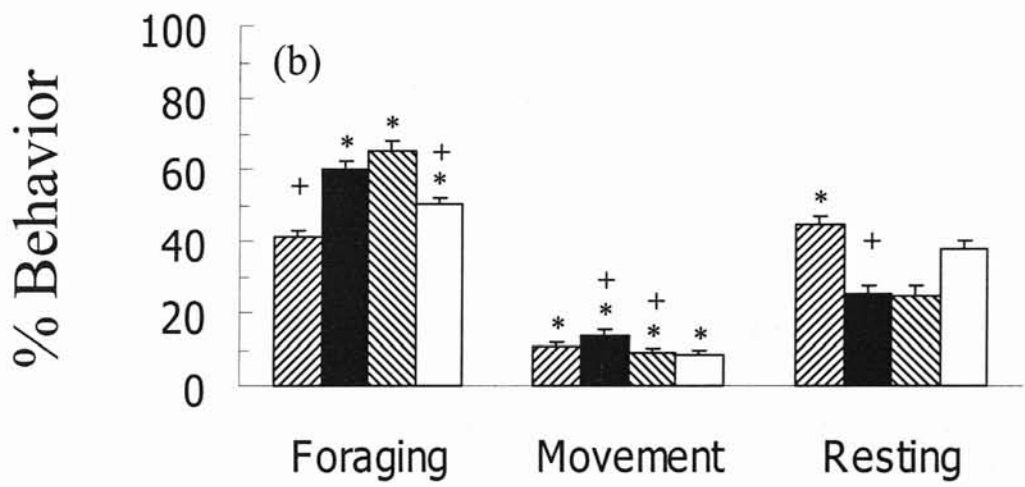
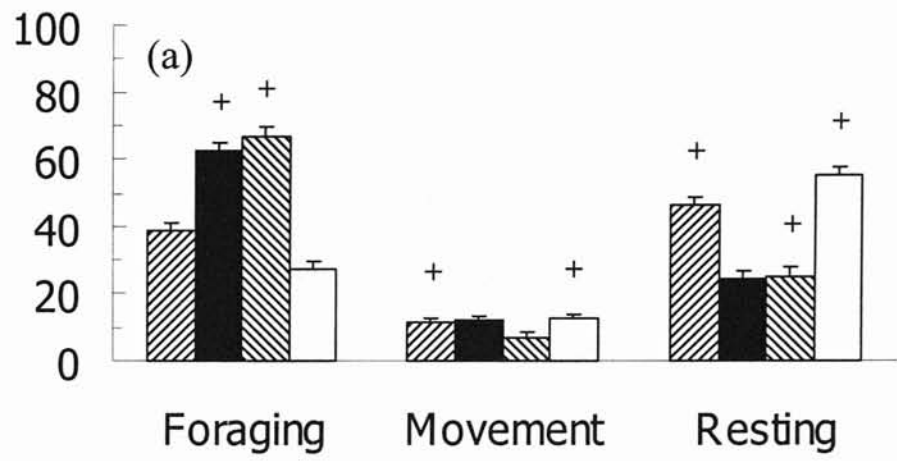
§ Wald's test; significance set at $P \leq 0.05$

APPENDIX B--FIGURES

Figure 1. Mean daily ambient temperature (°C) from concurrent behavioral samples every 30 min during summer (▲), spring (□), autumn (●), and winter (Δ) at Tallgrass Prairie Preserve, Osage County, Oklahoma.

Figure 2. Mean percent diurnal calf (a), diurnal adult (b), and nocturnal adult (c) behavior during summer (▨), autumn(■), winter (▩) and spring (□) at Tallgrass Prairie Preserve, Osage County, Oklahoma. "+" and "**" indicate significant difference between adults and calves within individual seasons (Chi-square tests: $\chi^2_1=16.70$ to 1116.44, $P<0.0001$ for all tests) and diurnal and nocturnal periods within seasons within adults (Chi-square tests: $\chi^2_1=126.65$ to 1314.69, $P<0.0001$ for all tests), respectively.





VITA

Eric Jason Maichak *2*

Candidate for the Degree of

Master of Science

Thesis: BEHAVIORAL VARIATION IN BEHAVIOR OF BISON (BOS BISON BISON) ON A TALLGRASS PRAIRIE

Major Field: Wildlife and Fisheries Ecology

Biographical:

Personal Data: Born in Oklahoma City, Oklahoma, on October 31, 1975, son of Mitchell M. Maichak, Jr. and Georgia L. Stump.

Education: Graduated from Del City High School, Del City, Oklahoma May 1994; received Bachelor of Science degree in Biology from the University of Arkansas, Fayetteville, Arkansas, August 1998; completed requirements for Master of Science degree in Wildlife and Fisheries Ecology from Oklahoma State University, Stillwater, Oklahoma, May 2002.

Professional Experience: Work/Study, Registrar's Office, Northwest Arkansas Community College August 1994 to May 1996; Graduate Teaching Assistant, Department of Zoology, Oklahoma State University, August 1999 to May 2002; Graduate Student Faculty Council Representative, Department of Zoology, Oklahoma State University, August 2001 to May 2002.

Professional Organizations: Oklahoma State Student and National Chapters of the Wildlife Society, Biodiversity Working Group of The Wildlife Society, Oklahoma State Zoology Graduate Student Society