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Endocrine and behavioral observations during transition of non-breeding into breeding season in female American bison (*Bison bison*)

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Abstract

This study provides endocrine data in relation to behavioral events during the transition of the non-breeding into the breeding season in American bison (*Bison bison*). Fecal progesterone metabolite patterns (20-oxo-P) were obtained in 13 adult female American bison and hormonal data were correlated with behavioral observations; i.e. copulation, male tending, female tail-up behavior and gestation length. Based on fecal progesterone metabolite patterns, the breeding season started between the middle of July and early August. Predictable short cycles reflected the transition from non-breeding to the breeding season; the luteal phase of these cycles was 4.10 ± 0.86 days. Copulations and female tail-up behavior were reliably associated with the hormonally detected ovulation. Male tending behavior was more loosely associated with hormonally detected ovulation. The observed hormonal pattern in the study females indicated that 9 of 10 pregnant cows conceived during the second ovulatory period in the breeding season. One other cow conceived during her third ovulatory period, and one cow did not conceive until later in the breeding season by beginning of October. Gestation duration was on average 266.30 ± 1.00 days. In summary, this study confirmed that the bison is a seasonally polyestrous species; the transition from the non-breeding into the breeding season was characterized by short cycles with low progesterone metabolite values.

Keywords: Bison; Non-invasive endocrinology; Gestation; Progesterone; Sexual behavior; Seasonality

1. Introduction

American bison (*Bison bison*) are kept in ranches for commercial purposes [1]. Bison are seasonally polyestrous animals [2–6] with a short rutting season of about 2 months and a peak in early August. Numerous studies have demonstrated that the pattern of urinary and/or fecal progestin levels is a useful indicator of luteal activity in American bison [2–7]. However, the hormonal profile during the transition of the non-breeding into the breeding season has not yet been described in detail. In addition, it is unclear whether bison females exhibit only one or several estrous cycles per mating season.

The bison mating system is characterized by male-dominance polygyny [8]. During the rut, males compete to form tending bonds with the females [9]. The bulls move through the herds, regularly performing olfactory

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Table 1
Reported gestation lengths in Bison

Species	Gestation period	Methodology	Source
Bison bonasus	264.3 ± 4.2 days (range:254–272)	Observed copulations and calving, $n = 132$	Krasinski & Raczynski, 1967 [12]
Bison bison	285 days	Estimated from embryo sizes ($n = 121$) with cattle embryo growth curves	Haugen, 1974 [13]
Bison bison	262–272 days	Observed copulations or inferred copulations (tail-up) and observed calving with possible 1 day error, $n = 28$	Rutberg, 1986 [14]
Bison bison	277.8 ± 3.3 days 276.6 ± 2.7 days 286.2 ± 4.0 days 292.5 ± 4.1 days for each year $n = 17$	Observed copulations or inferred copulations (tail-up) and observed calving with possible 3 day error, $n = 17 \times 4$	Berger & Cunningham, 1994 [15]
Bison bison	257 days	Observed copulation and calving, fecal progestins, $n = 1$	Rutley, 1995 [16]

checks at the genital region of cows and at urine patches to detect females in or near estrus [9]. Tending can be defined as the continuous efforts of the male to remain in close proximity to the female during a few hours up to a few days prior to copulation [10]. Immediately after copulation, the cow arches her back, expels vaginal fluids and semen from the vulva and holds her tail-up. After copulation, the bull may continue to tend for a few minutes up to several hours, until he leaves to search for another cow [11].

It is common to derive presumed conception dates in free-ranging bison from observed copulations or from indirect signs associated with copulation, i.e. the presence of a tending bull or the female keeping her tail in a horizontal position (Table 1). Gestation length is usually calculated as the interval between the last observed or inferred copulation and the subsequent birth date. Based upon this methodology, it has been suggested that American bison females show variable gestation lengths ranging from 257 to 293 days (Table 1) and that they are capable of facultative gestational length adjustment [15]. However, in the absence of hormonal data, the calculation of gestation length can be flawed to some extent in case copulations, or the behaviors used to infer the occurrence of a probable conception occur at non-fertile periods.

Reliable endocrine and behavioral indicators of conception can prove useful for captive herd management. This study was conducted during the rutting period in thirteen female bison in a larger herd with several adult males present. We examined sexual behavior (copulations, male tending and female tail-up behavior) in relation to the hormonally detected fertile periods. We suggest a reliable operational behavioral indicator of the probable timing of conception and, using behavioral and endocrine results, we determined gestation length.

2. Methods

2.1. Animals and herd management

The herd was composed of 42 adult American bison females held in semi-natural conditions on a commercial farm in the Belgian Ardennes. All females studied were imported at 1 year of age from the United States; the cows were 9 years old at the beginning of the study. The herd grazed year-round on meadows of about 25 hectare on average on a total surface of 180 ha (altitude: 580 m). In summer, three males (9, 4 and 2 years) were introduced to the group. During autumn and winter (middle of September until April) the pastures had only low grass productivity and therefore the herd was fed with additional mixed grasses hay. The animals were individually recognizable through an ear tag and phenotypic differences. Each year, calves were weaned in December at about 7 months of age and removed from the herd. During this roundup, all animals were weighed using a squeeze chute with a floor balance.

Most females had calves in 2001 and were lactating during the study period, except for #209, #230, and #244. In the subsequent year, all females but, #203 and #210 bore calves.

2.2. Behavioral observations

Thirteen animals were used for behavioral and hormonal monitoring. These study animals were selected within the highest and the lowest ranking section of the herd in order to cover the two extremes of the dominance rank. Observations were carried out from a four-wheel drive vehicle within the herd to which the animals were fully habituated. From 26 of May until 14 of September 2001 (325 h) all agonistic interactions

were scored. From 13 of June until 27 of October 2001 all observed sexual interactions were scored (255 h) on the study animals combining focal animal sampling (7 × 30 min/individual) and ad libitum scoring of all occurrences of agonistic and sexual behaviors of all herd members. For a list of agonistic behaviors see Vervaecke et al. [17]. During the rut, observations were carried out, on average, for 4 h/day on 6 days/week; the 4 h period was divided into two periods of 2 h—one in the morning and one in the afternoon. Behavioral observations in the herd did last for 8–10 h per day, but the additional time was focused on other aspects of male and female behavior and these additional results are presented elsewhere [17,18]. The following behaviors for the females were recorded; observations were carried out in close proximity to the animals in focus and were supported by use of binoculars:

- Tended by a bull: the bull remains in a close position and follows the female longer than 30 min, accompanied by one or more attempts to mount, by mounts, by licking or by chin on back behavior.
- Tail-up by the female: female holds the tail in a nearly horizontal position, more than just slightly exposing the vulva, during protracted periods of several hours up to several days, regardless of the context.
- Copulation: male mounts a female with intromission.

2.3. Collection of fecal samples

From the 13 female bison, fecal samples were, on average, collected twice weekly between the middle of June until the middle of September. Before and around rut (August) sampling frequency increased up to five samples per week. Thereafter samples were collected approximately once every 2–3 weeks until end of October. The samples were taken immediately upon observed defecation; before collection the feces was homogenized by stirring with a wooden spatula. Samples were put in plastic vials, labeled, stored in a cool box during the day of collection and then frozen at −20 °C.

2.4. Hormonal analysis

Fecal progesterone metabolites were analyzed after extraction using a group-specific enzyme immunoassay for 20-oxo-pregnanes (20-oxo-P) as described in Schwarzenberger et al. [19]. Using this assay in domestic cows, fecal 20-oxo-P concentrations during the follicular and luteal phase were 39.5 ± 2.2 and 341 ± 15.2 ng/g feces, respectively. Furthermore fecal 20-oxo-P concentrations were parallel to milk progesterone values, but had a lag time of about 0.5 days [19].

2.5. Definition of luteal phases and previous ovulations

A threshold value for the onset of the luteal phase was calculated using basal fecal 20-oxo-P-values taken from the non breeding season in the period from the middle of June (onset of the sampling) until the middle of July (before rut). From this period the mean ± S.D. of the 20-oxo-P values (n = 106) was 26.7 ± 13.2 ng/g feces. The threshold value was defined as three S.D. above the mean. For easy use in further analysis, the final threshold used to define the onset and the end of the luteal phase and to infer previous ovulation was set at 70 ng/g feces.

2.6. Definition of pregnancy

The beginning of pregnancy was defined on the basis of hormonal and behavioral results. Despite behavioral observations, copulation was not observed in all animals. Therefore the first day of gestation was defined as the last day on which copulation was observed or the day on which tail-up behavior was shown. This was accompanied by a subsequent rise and continuously elevated fecal 20-oxo-P values above the threshold of 70 ng/g feces.

2.7. Statistical analyses

Behavioral dominance rank analyses were carried out with MatMan software [20]. We calculated how many days tending behavior, copulations and tail-up behavior were shown and when these occurred relative to days of transgression of the 20-oxo-P threshold. As fecal samples were not collected every day, calculation of luteal phase length was based on the mean of values that were separated by 2–4 days. In one female (#203) there was a sampling gap of 8 days between observed tail-up behavior and the second transgression of the 20-oxo-P threshold. Therefore for this female the second transgression was not correlated to tending, copulation or tail-up behavior in relation to presumed second ovulation. The Spearman rank correlation coefficient was used to correlate dominance rank or weight with dates of first tending dates of presumed first and second ovulation and duration of tending. Results are presented as mean ± S.E.M. The critical significance level alpha was set at 0.05. All reported p-values were two-tailed.

3. Results

3.1. Transition from non-breeding into breeding season

Detection of ovulation was based on 20-oxo-P-levels and results are shown in Fig. 1 and 2. Basal 20-oxo-P-values indicative of the anestrous period were observed in June and July. This was followed by short cycles with low 20-oxo-P-values. It is assumed that these short luteal phases were subsequent to the presence of the first ovulatory follicles and thus indicated the transition from non-breeding into breeding season. Maximum 20-oxo-P-values during these short cycles were in the range of 100–300 ng (mean ± S.E.M. was 147.2 ± 35.2) and thus were well above the threshold value (70 ng/g feces) for the definition of the luteal phase. These short cycles occurred in all cows between the last third of July and the middle of August. Definite results were obtained in 10 animals; 20-oxo-P-values were approximately 70 ng/g feces in three cows (# 204os, # 210, # 222). The length of the luteal phase of these short, transitory cycles was 4.1 ± 0.9 days ($n = 10$). The first three females to show luteal activity were # 209, # 230 and # 244, the three only non-suckling females. After these short cycles, fecal progesterone metabolites increased significantly in all 13 animals and thus indicated the second ovulatory period. This second ovulatory period, as indicated by observed mating, tail-up behavior and fecal 20-oxo-P-values occurred between the 3rd August and 1st September; in seven of the 13 cows, this period was observed between the 9th and 13th of August.

On average, tending by a bull was observed during 3.3 ± 0.4 days throughout the entire mating period (first and second ovulatory period combined). Six females were tended prior to the first luteal phase, and all females were tended prior to the second luteal phase. However, tending in several females occurred also during luteal phases and also during early pregnancy and thus tending was not a reliable indicator of behavioral estrus.

Based on fecal 20-oxo-P-values, the length of the second ovulatory period was 5.9 ± 0.3 days (range 4–7 days). Six copulations were observed in six females; five of these were noticed in the second ovulatory period; the other copulation was observed in female #230 in her 3rd ovulatory period. Copulations occurred on average 1.7 ± 0.4 days (range 1–3 days) after the end of the previous luteal phase, and 3.9 ± 0.4 days (range 3–5 days) prior to the start of the subsequent luteal phase. Females were observed to keep their tail-up during 1.7 ± 0.3 (range = 1–4) days on average. The last day of tail-up behavior was on average 3.2 ± 0.3 (range = 2–4) days prior to the start of the subsequent luteal phase.

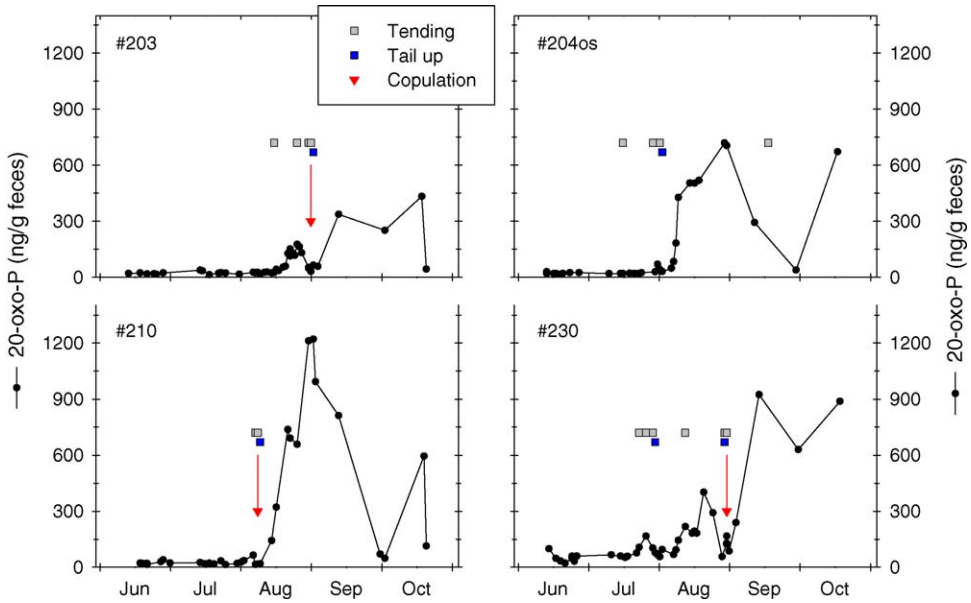

Fig. 1. Profiles of 20-oxo-P metabolites in female bison. Cows #203 and #210 were non-pregnant in the subsequent year, but as indicated by endocrine results these two females possibly did resorb the embryo. Cow #204os did conceive by beginning of October. Cow #230 did conceive in her 3rd ovulatory period by end of August; this cow was non-lactating. Behavioral observations included (■) tending by a bull, (■) tail-up behavior of cows, and (▼) observed copulations in some cows.

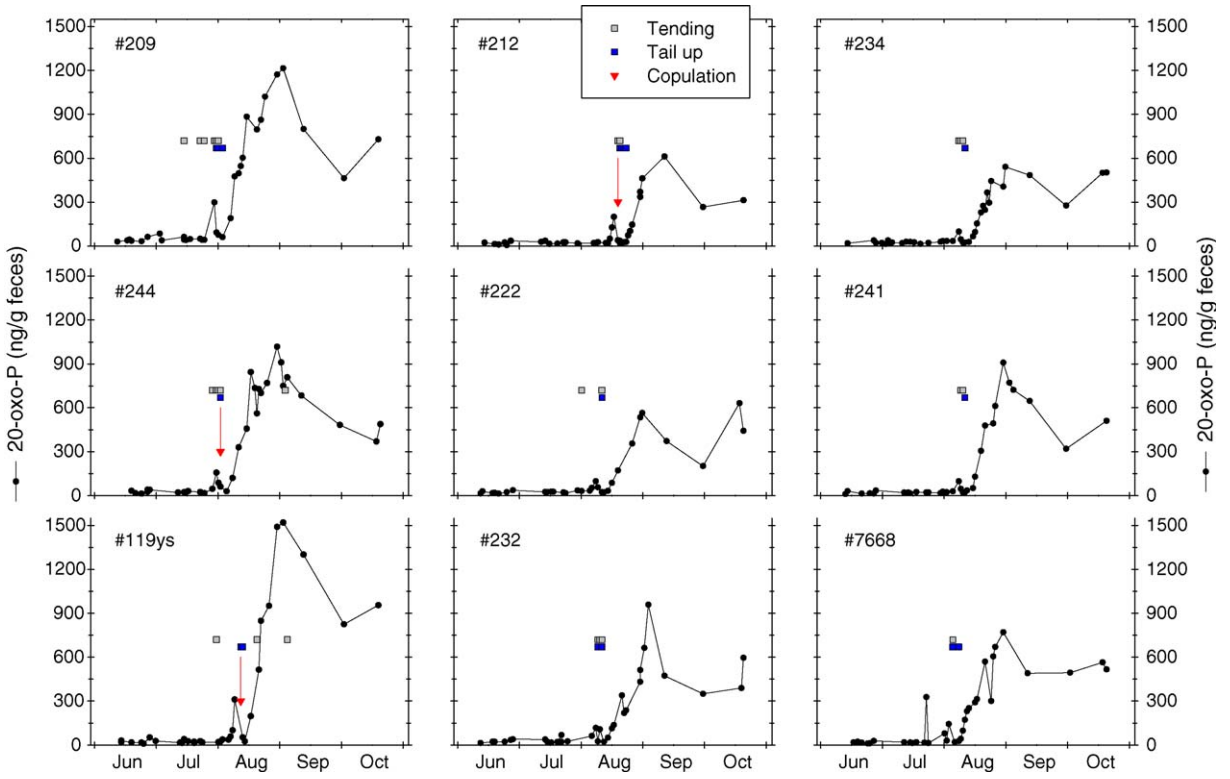

Fig. 2. Profiles of 20-oxo-P metabolites in pregnant female bison. Cows # 209 and #244 were not lactating during the study year. The other cows had calves during the study year and were lactating. Behavioral observations included (■) tending by a bull, (■) tail-up behavior of cows, and (▼) observed copulations in some cows.

3.2. Calculation of gestation length; correlation between behavioral and endocrine results

Most (9 of 10; Fig. 2) pregnant females conceived during the 2nd ovulatory period. Female #230 (Fig. 1) conceived in her 3rd ovulatory period by end of August and delivered a calf after 272 days of gestation; 20-oxo-P-levels between the second and the third ovulatory period in this animal indicated a luteal phase of 18 days in length. Three other females (#203, #210, #204os; Fig. 1) either did not conceive or resorbed the fetus. As indicated by a drop in 20-oxo-P-levels and barrenness in the subsequent year, females #203 and #210 possibly resorbed the fetus after 5 and 7 weeks, respectively. The 20-oxo-P-values indicative of early gestation in female #204os dropped between day 40 and day 58 (1st of October). As implied by 20-oxo-P-values, female #204os conceived again by beginning of October and calved on the 4th of July after a gestation length of about 265–275 days.

Gestation length was on average 266.30 ± 1.00 days (range: 262–272; median = 267 days, $n = 10$). Female #204os was not included in this calculation, as the exact gestation length could not be determined. Nine of the cows calved between the 22nd of April and 17th of May; cow #230 calved on the 29th of May and cow #204os calved on the 4th of July.

Behavioral and endocrine results were correlated with rank and weight; when appropriate the three non-suckling females were excluded. Rank and weight were significantly correlated ($r = -0.82$, $p = 0.01$, $n = 13$). Female weight correlated significantly with the number of days tended by the bull ($r = 0.55$, two-tailed $p = 0.05$, $n = 13$); but this was not so for high ranking females ($r = -0.28$, $p = 0.35$, $n = 13$). High ranking and heavier females showed a trend towards earlier tending by the bull, however, these correlations were not significant (rank-first tending: $r = 0.37$, $p = 0.26$, $n = 10$; weight-first tending: $r = 0.20$, $p = 0.54$, $n = 10$). In accordance with the behavioral data, there was a statistical trend for the higher ranking females to show earlier luteal activity ($r = 0.61$, $p = 0.05$, $n = 10$), but this was not so for heavy females ($r = 0.28$, $p = 0.54$, $n = 10$). A partial correlation between rank (x) and date of start of luteal activity (y) corrected for weight (z), strengthened this result ($r(xy.z) = 0.51$, $r(xz.y) = -0.64$, $r(yz.x) = 0.18$, $n = 10$),

indicating a genuine rank effect. With regard to the start of the second luteal activity, there was no significant correlation between rank or weight and conception date.

4. Discussion

The transition from non-breeding into breeding season was characterized by short cycles with low progesterone metabolite values. These short transition cycles have not yet been described for bison, but domestic cows have a comparable progesterone profile when they resume ovarian activity after parturition [21,22]. Suckling a calf, nutrition, season and age (parity) are factors that can increase the duration of the postpartum anestrous in cows [21,22]. In our sample the first ovulations were seen in females that were not suckling calves. The males directed their first sexual interest towards these females, as also observed in previous studies in bison [23]. In dairy cows it was found that females in a negative energy balance had low estrogen and low progesterone secretion and a larger number of abnormal cycles [24,25]. We found that not weight but female agonistic rank was related to early luteal activity. This suggests that in bison, as well as in domestic cows, a complex of intertwined factors such as weight, rank and energy balance (among other factors such as age and genetics) may affect the female attractiveness and her reproductive functions [21–29].

Synchrony of the 2nd estrus during the breeding season was high in the study females, confirming the finding by Wolff [11] with 90% of the females showing estrus in a period of 4–6 weeks. In our study, the second ovulation was always accompanied by estrus behavior, which was not so for the first ''transition'' ovulation. We found, that on average, the copulations occurred 3.9 days, and the last day of tail-up behavior 3.2 days prior to the second observed luteal phase. In cows, mounting was the best predictor for time of ovulation (occurring 28.7 ± 5.3 h before ovulation) [29], and milk progesterone concentration reached 1.0 ng/mL within 5 days after insemination [30] and fecal progesterone metabolites were shown to be parallel to milk progesterone levels with a delay of about 12 h [19]. Inferred from these results, it seems likely that in cows and bison the timing of the events between estrus behavior, ovulation and luteal development is comparable.

We found a consistent rise in 20-oxo-P-levels upon conception, which remained elevated throughout gestation, thus providing a reliable indication of luteal function and pregnancy. In contrast, Kirkpatrick et al. [3] found that pregnancy determination in bison based on fecal testing of progesterone was not reliable until the 3rd month of gestation. Rutley [16] also found that during the first 48 days post conception fecal progestins did not differ between pregnant and open females. The probable reason for this different result is the specificity of the progesterone assays used. In a variety of animal species, progesterone is metabolized to several pregnanediones and to mono- and dihydroxylated pregnanes before it is excreted in the feces, while intact, unmetabolized progesterone is barely present, if at all. Therefore, if used for the analysis of fecal progesterone metabolites, rather specific progesterone assays underestimate the concentration of cross-reacting fecal progesterone metabolites [19].

The hormonally confirmed gestation period in this study ranged from 262 to 272 days. This is in correspondence with the ranges given by other authors [12,14] but it also deviates by about 1–2 weeks from findings cited in Table 1 [12,13,16] All of the observed presumed resorptions of the fetus in our study occurred prior to or around the period of implantation, which is known to occur around day 42 in cattle [31].

Overall, tending behavior was only loosely associated with presumed ovulation and conception and we conclude that a certain error can be expected when tending rates are used to estimate timing of conception. Several females showed multiple tending bouts during days apart from the presumed ovulation or during pregnancy. This is in line with previous observations by Komers et al. [7] who observed a female in a tending bond while she was several days away from estrus. However, our interpretations differ somewhat from Kirkpatrick et al. [5] and Komers et al. [7] who proposed male tending behavior as reliable indicators of ovulation. It has been suggested that some of the inter-individual difference in estrus duration as expressed in mounting and tending may be explained by differences in female weight [32]. In our study, males indeed tended the heavier females during a higher number of days. Thus for heavy females, tending may be a less precise indicator of ovulation than for females with lower body weight.

We observed copulations in only half of the focal females. However, tail-up behavior was observed in all study females in close association with presumed ovulation as indicated by hormonal data. Tail-up behavior may last for 4 days and it corresponds closely in time with the copulation. However, a distinction should be made between complete tail-up and moderate elevation of the tail. The latter behavior can be observed in females that were approaching ovulation. They lift the tail moderately when the bull is in the area but the tail resumes its normal lower position when the context

alters. Complete tail-up behavior is defined as a nearly horizontal position of the tail. In most cases this behavior is associated with visible signs of semen and vaginal fluids at the vulva or on the buttocks. Based on the strong consistency of the association between fecal progesterone metabolites, tail-up behavior and either copulation or signs of semen, we conclude that it is a reliable indicator of a recent copulation.

There is some uncertainty as to whether bison females show more than one estrous cycles per mating season. Rutberg [14] reports that bison cows from the National Bison Range did copulate only once per season. Lott [10] reports that one cow in five will stand for another mounting during one breeding season, and that this is almost always a cow that bred near the end of the breeding season. Based on the examination of corpora lutea ($n = 148$ ovaries) from slaughtered bison, Haugen [13] claimed that a second estrus and ovulation per year is rare among bison. However, there is evidence for the occurrence of multiple estrous cycles in wood bison. Using urine and fecal hormone analysis, consecutive, multiple estrous cycles with mean cycle duration of 21.1 days (range: 16–31 days) were observed [3]. The authors concluded that this species is seasonally polyestrous when conception is prevented by the absence of a bull. Similarly, Kirkpatrick et al. [2] reported that seven of eight monitored female bison kept in a semi-free roaming commercial herd in the presence of six mature bulls feeding on natural grass became pregnant only in the second estrous cycle detected by urinary pregnanediol-3-glucuronide (mean cycle length = 23.1 $\pm$ 0.7 days; range: 19–26 days).

Our study shows that in the presence of three males and in well-nourished conditions, most females conceived from one mating in their second ovulation; this was associated with the majority of the observed sexual behavior. Only one female did not conceive during this second seasonal ovulatory period, but copulated and conceived 1 month later in her 3rd ovulatory period, thus confirming that the bison is a seasonally polyestrous species.

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