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Defecation rate in captive European bison, *Bison bonasus*

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Abstract Data on the digestive characteristics of European bison, *Bison bonasus* (L.), are needed for studies of their role as the largest extant herbivore in Europe and a potential keystone species of the temperate forest ecosystem. Very little published data are available, particularly on the defecation rate which affects population estimates from dropping counts and also the individual seed deposition rate. We gathered data from a captive bison group kept at the Show Reserve of the Białowieża National Park. Droppings accumulated in the enclosure over a 72-h period were counted in winter 2010. In addition, the group was observed over approximately 6-h periods three times in winter and 16 times in summer. The count of accumulated droppings over a 72-h period gave eight defecations per day. The summer direct observations recorded 7.5 defecations per day and winter observation 5.4 defecations per day. These estimates are within the range for other bovids of similar size. The difference between summer and winter observation-based estimates may be accounted for by a higher frequency of defecation in early morning and late afternoon, periods not covered in winter observations. Given the published density of seedlings emerging from droppings of the ~470 free-living bison in the nearby forest, eight defecations a day mean that seed deposition by European bison may contribute significantly to realize seed dispersal and plant establishment.

Keywords Behaviour · Seed dispersal · Endozoochory · Białowieża forest

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Introduction

As part of nutrient cycling and digestive physiology, defecation is of intrinsic interest. In ungulates especially, the defecation rate is also important to managers using pellet groups to enumerate population sizes (Hemami and Dolman 2005; Camargo-Sanabria and Mandujano, 2011) and also ecologists studying the dispersal of seeds, as ungulates are the main spatial dispersal vector of a wide range of species (e.g. Cosyns et al. 2005; Eycott et al. 2007). The number of seeds can be enumerated from droppings collected in the field, but to understand the seed dispersal potential of an individual animal, the daily defecation rate must also be known (e.g. Poulsen et al. 2001; Graham et al. 1995).

The European bison, *Bison bonasus* (L.), is the largest free-ranging mammal in Europe (although a very rare one). The Lowland European Bison population (ssp. *Bison bonasus bonasus*) became extinct in the wild in 1919 (Krasińska and Krasiński 2007) and has been restored over the past 8 decades from captive individuals, with the largest free-living population by far being in the Białowieża Forest. The European bison in Białowieża Forest have been shown to disperse a very high number of seeds in their droppings (Jaroszewicz et al. 2008; 2009). However, there were only

473 individuals in the Polish part of Białowieża Forest at the end of 2010 (Raczyński 2010) compared to over 5,000 *Cervus elaphus* (Kuijper et al. 2010), which suggests that bison may not disperse the greatest number of seeds per unit area of the forest. To understand better their contribution to the forest per animal, it is necessary to enumerate their defecation rate.

We were unable to find any empirical observations of European bison defecation rate. We therefore used a group of captive bison at the European Bison Show Reserve of the Białowieża National Park to provide an estimate of defecation rate to use as an approximation for rapid population estimation and seed dispersal modelling. Activity budgets were made in order to make future comparisons between the captive herd and free-living individuals and explore the hypothesis that defecation might be linked to specific activities such as rumination.

Methods

The study was conducted in winter 2010 and summer 2011. During our investigation, a group of ten bison were kept at the Show Reserve—an area where the public are able to observe the animals of the forest in large enclosures. In winter, the group consisted of one mature bull, five mature cows, and two male and two female juveniles born in summer 2010. In summer 2011, the group consisted of the same individuals minus two juveniles and plus two calves born that summer (0–2 months old during the observations). These group compositions are similar to that of free-living bison groups, with only juveniles of 2–3 years lacking (Krasińska et al. 1987). The bison lived in a 6.14-ha enclosure of grass with occasional trees, which is divided by robust fencing into four equal sections. During the day they were kept in one section, and overnight they had freedom to move between two sections, with the remaining two sections unused.

We employed two methods of counting: counting of accumulated dropping piles and direct observation of defecation. In order to count accumulated droppings, the bison were moved into the 'spare' pair of enclosures after an accumulation of approximately 30 cm of snow. Prior to this, the 'spare' enclosures had not been used by the bison for several weeks, since before the first snowfall of the winter. After 72 h, the bison were moved back into the 'main' pair of enclosures, and the droppings were counted in the vacated enclosures; they were clearly visible in the snow. To avoid counting droppings twice, each dropping was marked. Five people walking in a line surveyed each enclosure systematically for 30 min, then freely for a further 10 min.

In winter, the direct observation periods were approximately 6-h long, running from around 9 a.m. to around 3 p.m. (17 h in total in December 2010). The bison were observed continuously using two observers. In the summer recording period, observations ran from 7 a.m. to 1 p.m. one day, then from 1 p.m. to 7 p.m. the next day, repeated eight times (96 h in total between 20 June and 18 July 2011).

Activity pattern was observed as scan sampling: the activity was recorded every 15 min for adults and every 5 min for calves and 1-year olds, and all defecations were recorded by continuous observation. We noted which animal defecated; only five defecations recorded could not be assigned to an individual. Behaviour (standing, lying, foraging on grass and woody material, feeding on food supplied by managers and mother–calf interactions such as nursing), especially whether rumination was apparent from jaw movement or salivation, was recorded in order to explore the hypothesis that defecation was linked to other digestive behaviour such as rumination (Krasińska and Krasiński 2007).

The bison are fed as their enclosure is too small to provide adequate food, and their diet may affect their defecation frequency. In winter, the diet is more 'artificial' than in the summer. The winter feeding regime for these captive animals was as follows: in the morning, at around 8:30, bison were fed 2 kg of crushed grain (oats and maize) per adult and 0.5 kg of crushed grain per calf. At 11 a.m., the group was given about 40 kg of beetroots. At 4 p.m., they were again fed, with the same amount of grain and 10 kg of hay per adult and 3 kg of hay per calf. In summer, the feeding of bison in the Show Reserve is much closer to their natural diet—the basic food is pasture, supplemented with crushed oats and corn (4 kg per adult per day, 1.5 kg per juvenile per day, calves no supplement), and additionally, some browses are provided (cut twigs and leaves). As the bison group is given grain all year round and hay and beetroots were introduced a few weeks prior to our winter recording, the digestive process of observed animals should not have been unsettled during either period of investigation.

Statistical analyses were carried out in the R base package (R Development Core Team 2011), using paired-sample *t* tests to compare summer to winter and daytime to morning and evening, with individuals as replicates.

Results

In the dropping accumulation survey, we counted 237 dropping piles, amounting to approximately eight droppings per animal per 24 h.

Over the 17 h of winter observations, 38 defecation events were observed (of which 33 could be assigned to individuals) equating to 5.4 defecations per animal per day (Table 1). In the summer observations, 301 defecations were

Table 1 Defecation rates from daytime direct observations of captive European bison

Age/sex class	Defecations per day (24-h period): mean for age/sex class (SE in parentheses; individual as replicate)	
	Winter (17-h observation)	Summer (96-h observation)
Adult male	11.28 (−)	7.75 (−)
Adult female	5.14 (1.29)	8.55 (0.33)
Juvenile	2.52 (0.91)	7.63 (0.88)
2011 calf	Not present	4.75 (0.25)

recorded over a 96-hour period, equating to around 7.5 defecations per animal per day (Table 1). A significant difference between summer and winter hourly rates could not be detected (t_7=−2.19, P=0.064). However, in summer, a greater number of defecations occurred in the early morning or late afternoon than in the daytime (t_9=−2.67, P=0.025), and defecations during those times would not have been recorded in winter.

In winter, the bull defecated most frequently while tending females (four defecations out of eight), and the cows did the most defecations while resting (5 defecations out of 18). In summer, the calves defecated most frequently during resting (25 out of 38 defecations), the juveniles and cows during eating (32 of 60 defecations and 73 of 171 defecations, respectively), and the bull defecated relatively evenly during all activities.

Discussion

Our methods produced estimates of defecation rate of between five and eight defecations per day, and it is likely that the actual figure is in the upper part of that range. For comparison, pasture-fed dairy cattle (*Bos taurus*) defecation rates range from 6 to 12 times per day (Oudshoorn et al. 2008), and captive American bison (*Bison bison*) bulls kept in pasture may defecate hourly (Herrig and Haugen 1969). The only estimate of defecation rate for European bison that we could find was a note suggesting one defecation per day (Krasińska and Krasiński 2007).

Our estimate of defecation rate gained from winter direct observation may be lower than that estimated from the winter accumulation survey and summer observation simply due to low sample size and random variation or more likely because of sampling—all of our winter observations were performed between 9 a.m. and 3 p.m. In summer, animals defecated more frequently in the mornings and late afternoons, and there may be links between defecation and other time-linked behaviours (e.g. Aland et al. 2002). We could not extend our recording period in winter due to lack of daylight. The defecation rate is lower for the calves because although calves begin foraging at 1–2 weeks of age, milk continues to form an important part of the diet for several weeks (Daleszczyk 2004; 2005).

Our data may not be directly comparable to rates in the wild as the bison we observed were captive and fed an artificial diet, particularly in winter. Artificial diets have been shown to affect digestion parameters in other ungulate species, with high-quality food reducing the time spent feeding on and digesting food. For example, *Bison bison* yearlings on a similar enclosed grass pasture reduced foraging time by 4 % when supplementary hay was supplied (Rutley and Hudson 2001). Between 35 and 48 % of time was spent foraging during recording hours in both summer and winter (in extensive grassland conditions, *Bison bison* also spend up to 45 % of their time foraging; Mooring et al. 2005). Grass pellets reduce digestive transit times in moose (*Alces alces*) by 30 % compared to mixed woody browse (Schwartz et al. 1988), and sheep in pastures defecate more frequently if their diet is supplemented (Pompeu et al. 2009).

European bison in the wild feed frequently on grasses but more frequently trees and shrubs (Caboń-Raczyńska et al. 1983; Gębczyńska et al. 1991), especially in winter when woody browse constitutes up to two-thirds of the diet (Kowalczyk et al. 2011) and is highly selected for in cafeteria experiments (Borowski and Kossak 1972). Even those free-living individuals who depend on the hay supplied by managers in winter do not have daily access to high-quality food such as corn and beetroots, as the Show Reserve group do in winter. The high-quality winter food would, therefore, be expected to increase defecation frequency in our study group as compared to the summer rate (and to wild individuals), but winter defecation frequency was not higher than summer frequency.

An alternative explanation for the difference between the winter observed frequency and winter accumulation data is that in the accumulation survey we may have counted older droppings. Some of our five observers suggested that they recorded one or two droppings which looked drier or less green. Still, this means our estimate from the dropping accumulation survey could overestimate the defecation rate by at most 4 % (less than one dropping per day).

European bison have received attention in the scientific literature due to their place as the largest extant 'wild' herbivore in Europe. As the data were collected under 'non-wild' conditions, we stress that our data provide only an estimate of the defecation frequency needed for population counts. However, we will be able to compare our estimates when activity budget data become available from currently radiocollared free-living individuals (R. Kowalczyk, pers. comm.)—if the captive and free-living bison spend similar amounts of time foraging and resting, it may be suggested that their diets may be similar enough to compare digestive parameters.

Our estimate is, therefore, a step towards a more mechanistic understanding (*sensu* Cousens et al. 2010) of endozoochorous seed dispersal by bison. Regarding the role of bison role as seed dispersers of forest plants, around 11 seedlings germinate from each dropping (Jaroszewicz et al. 2008). As an approximation, each bison may account for around 90 new seedlings per day (from eight droppings), over 40,000 seedlings per day in total for all the free-ranging bison in the forest. Bison core areas are very large, but the distribution of bison through the forest is uneven (mean 95 % kernel density is 40 km^2; Kowalczyk 2010), so they could be playing an important role in the spatial patterns of seed deposition and quite possibly plant establishment.

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