Gastrointestinal parasites of a reintroduced semi-wild plains bison (*Bison bison bison*) herd: Examining effects of demographic variation, deworming treatments, and management strategy

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A B S T R A C T

Bison (*Bison* spp) are being reintroduced into semi-wild, spatially constrained herds across North America and Europe. Herd managers are concerned about gastrointestinal (GI) nematode parasites as they care for the health of their bison. We examine how demographics, grazing location, herd management, and anthelmintic treatments affect the fecal egg counts (FECs) of GI nematodes within a reintroduced Plains bison (*Bison bison bison*) herd in the Great Plains. Our results suggest that younger bison (<2 years of age) experience higher GI parasite eggs/ oocysts per gram (epg/opg) and that some taxa are more prevalent throughout different periods of a bison's early years. Demographic findings suggest that calf and yearling (0–2 yrs age) bison have the highest FECs and that these decline until reaching a low in peak adulthood and thereafter (x > 6 yrs of age). FECs of both *Trichuris* spp. and particularly *Nematodirus* spp. were much more abundant, relatively, during the first year of a bison's life. This pattern was also true of *Moniezia* spp. and *Eimeria* spp., however, strongyle-type spp. FECs appeared to peak in relative abundance during the second year of life. Our data also indicate that FECs are influenced by differences in land-use histories of pastures previously grazed by cattle or by the proportion of frequent flooding in different pastures. Treatment results suggest that fenbendazole may more effective than moxidectin at lowering FECs of bison over the long-term, and lasting effects of at least one administered anthelmintic treatment. Multiplex PCR assays revealed that American bison share GI nematodes with cattle including: *Ostertagia* spp., *Haemonchus placei*, *Cooperia onchophora*, and *Oesophagostomum* spp, but did not detect the presence *Trichostrongylus columbriformis*. Our results may have wider conservation implications for reintroduction efforts of American bison, as well as the endangered European bison (*Bison bonasus*).

1. Introduction

Formerly numbering in the tens of millions, both extant subspecies of American bison (*Bison bison*), wood bison (*B. bison anthabascae*) and Plains bison (*B. bison bison*), were anthropogenically driven to near extinction by the late 1800's (Shaw, 1995). Today, American bison numbers have recovered substantially to more than 500,000 across North America; however, only ~4% of the population are managed as conservation herds (Carter and Matheson, 2017). Continuous reintroduction efforts are being made to recover both American bison subspecies and European bison (*Bison bonasus*) and to rewild landscapes and

ecosystems (Pucek, 2004; Sanderson et al., 2008). However, these herds face distinct challenges including movement restrictions, genetic isolation, and proximity to livestock, which can promote disease and parasite transmission (Tessaro, 1989; Pucek, 2004; Freese et al., 2007). The critically endangered European bison shares a similar history of near extinction, reintroduction efforts, threats, conservation challenges, and recovery strategies as American bison (Pucek, 2004; Plumb et al., 2020). Some bison currently exist as smaller, less defined herds that can contribute to the long-term conservation of the species (Truett et al., 2001; Pucek, 2004; Sanderson et al., 2008; Gates and Aune, 2010). Small, conservation-oriented herds can promote species resilience by

serving as field laboratories for research into bison disease-ecology and other important topics, providing adaptive frameworks for developing best management practices (Karesh and Cook, 1995; Nishi et al., 2006).

Both European bison and American bison are exposed to parasites that are similar to cattle (Knapp, 1993; Demiaszkiewicz et al., 2009, 2010); however, some evidence suggests that American bison are infected at higher rates than cattle (Avramenko et al., 2018). Recommended best practices for American bison and European bison management and recovery include diagnosis of gastrointestinal (GI) parasite infection levels and efficiency testing of anthelmintic treatments (Pucek, 2004; Carter et al., 2010; Kaplan, 2013). Production loss, clinical disease, and mortality due to parasitism in the commercial cattle and bison industry have led to routine deworming becoming a common practice for bison managers in North America and Europe (Wade et al., 1979; Hennings and Hebbring, 1983; Eljaki et al., 2016; Woodbury et al., 2014; Kryzsiak et al., 2015). However, questions still surround the effectiveness and need for drug treatment in bison, especially in conservation-oriented, semi-wild herds (Dies and Henderson, 1998; Woodbury et al., 2011), because drug resistance has developed from long-term routine use of parasitic treatments (Kaplan and Vidyashankar, 2012; Kaplan, 2013; Jones et al., 2014; Pyziel et al., 2018) and because of the potential for parasite transmission between domestic and wildlife ecosystems (Barone et al., 2020).

Though several studies have been done regarding bison GI nematodes (Roudabush, 1936; Zaugg, 1993; Van Vuren 1995; Kolodziej-Sobocińska et al., 2016), relatively few have focused on demographics, management regimes, or long-term treatment effectiveness (Ryff, 1975; Penzhorn, 1994; Marley, 1995; Dies and Coupland, 2001; Woodbury et al., 2011; Eljaki et al., 2016). More information on geographical distribution and diversity of GI nematodes in American bison is also needed, especially in understudied landscapes throughout their historical range (Woodbury et al., 2014; Avramenko et al., 2018).

We examine temporal and demographic variation in GI nematode fecal egg counts (FECs) of a reintroduced Plains bison herd in response to land use history and land management practices. We also explore the effectiveness of moxidectin (administered topically through a pour-on solution) and fenbendazole (administered orally through ingestible pellets) anthelmintic treatments over extended periods of time to detect the real-world impacts of treatments on egg/oocyst production as they are practically applied by conservation bison managers. We also report on strongylid-type GI nematode species diversity of bison within the central Great Plains. More information on regional distribution, effectiveness of management regimes, and the development of natural immunity to GI nematodes will aid in generating new practices for production, semi-wild, and conservation bison herds in Europe and North America alike.

2. Methods

2.1. Fecal collection

The Crane Trust (CT) owns and manages ~6000 acres of lowland tallgrass prairie, wet meadow, and riparian land as critical Whooping Crane (*Grus americana*) and migratory bird habitats along the Platte River in southcentral Nebraska (40.78° N, −98.47° W, 600 m elevation) (Currier, 1982, 1989; VanDerwalker, 1981). The biological integrity of the grassland landscape is maintained by use of controlled fires, tree removal, haying, and grazing (Currier, 1997; Fuhlendorf, 2009). Plains
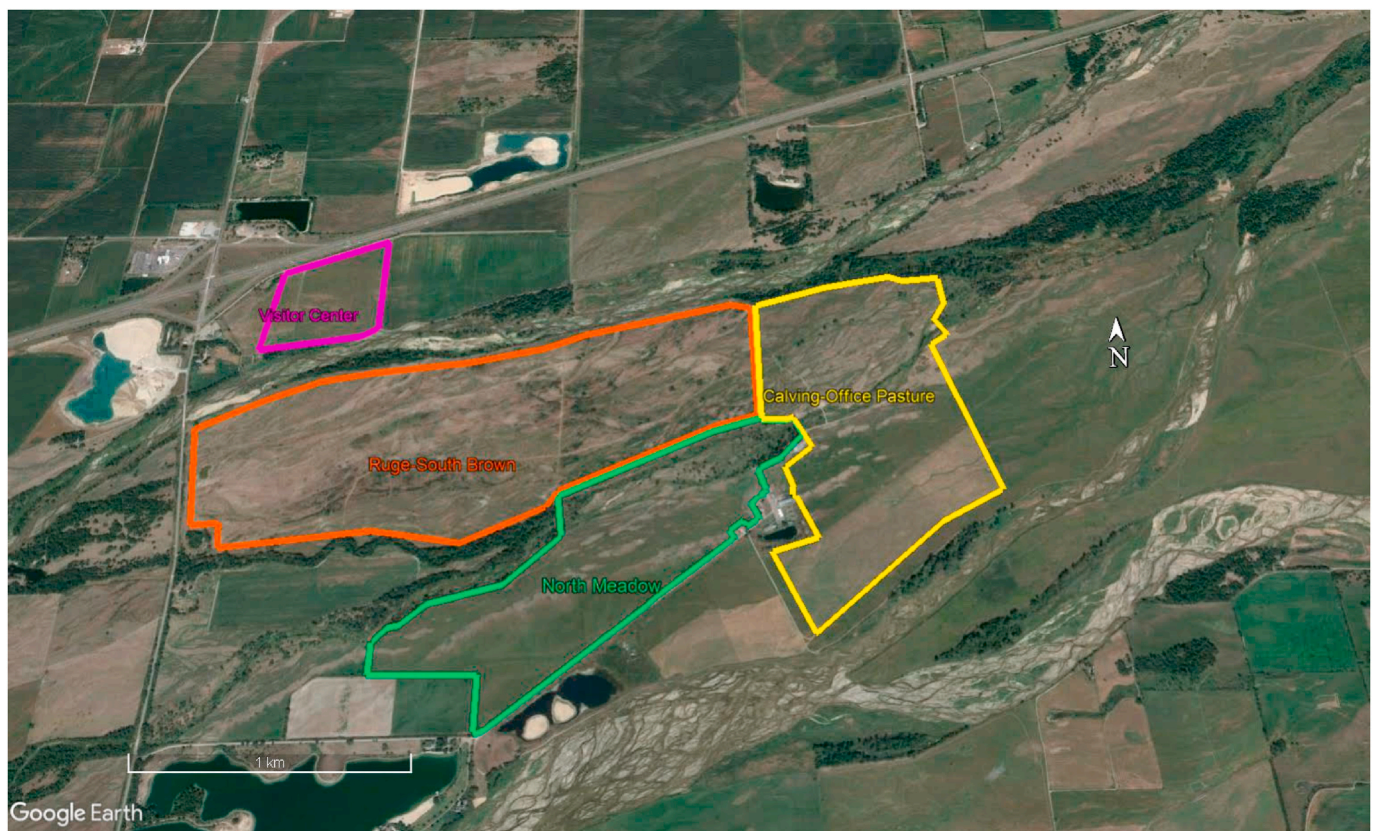
Fig. 1. Aerial image of the Crane Trust bison pastures. The smaller North metapopulation was continuously grazed in the Visitor Center ("VC" – 50 acres) pasture (outlined in pink). The larger South metapopulation was rotated through Ruge-South Brown ("RS" – 387 acres) pasture (outlined in orange), Calving-Office ("CO" – 267 acres) pasture (outlined in yellow), and North Meadow ("NM" – 177 acres) pasture (outlined in green). The North (orange) and South (pink) metapopulation pastures were separated by a minimum distance of 200 m, including an 80 m channel of the Platte River. (For interpretation of the references to color in this figure legend, the reader is referred to the Web version of this article.)

bison ("bison" throughout methods and results sections) were reintroduced as a new grassland management strategy (Truett et al., 2001), opting to have a native ungulate instead of cattle on a portion (881 acres) of its property (Fig. 1). These bison exist as one semi-wild bison herd treated as two separate metapopulations for genetic management purposes. These metapopulations vary by herd size, stocking rate, grazing regime, and accessible acreage. The South metapopulation is larger (n = 37–87 bison) and was reintroduced in January 2015, inhabiting 831 acres with rotational grazing between three parcels (Ruge-South Brown, North Meadow, Calving-Office Pasture). The North metapopulation is smaller (n = 7–15 bison), reintroduced in February 2014, inhabiting 50 acres with continuous grazing on one parcel (Visitor's Center) of lowland tallgrass prairie reconstructed from a previous agricultural field. During the study, the bison metapopulations were kept separate and were not mixed to prevent the direct transfer of GI parasites between the metapopulations to study the effects of grazing strategy and land use history. Additionally, the metapopulations were separated a minimum of 200-m between grazing pasture boundaries including an 80-m-wide channel of the Platte River (Fig. 1). Each parcel (Fig. 1) varies based on different land use histories and proportion of total area frequently or occasionally flooded (Table 1).

2.2. Sampling design

Bison fecal samples were collected from November 18, 2015 to September 3, 2019. From 2015 to 2017 samples were collected during annual bison working periods in October or November by collecting fecal droppings from the compression chute or by manually extracting samples from the bison rectum. Beginning in 2018 samples were also collected in-the-field throughout the year where animals were observed defecating using binoculars and then samples were collected off the ground and labeled by individual tag number or by identifying features.

The relationship between FEC and worm burdens has been somewhat tenuous. In sheep and goats, this association shows reasonable predictability (Cabaret et al., 1998); however, in large ruminants the relationship between worm burdens and FEC is not as well established (Forbes, 2017). Still, given that infections are not synchronic but acquired on a recurring basis, diagnosis using DNA methods on fecal eggs correlate well with the presence of adult worms in the GI tract (Eysker and Ploeger, 2000). FECs were conducted at two different locations, i.e. CT and the University of Nebraska-Lincoln Veterinary Diagnostic Center (UNL) using the same methods. Centrifuge flotation method was chosen because it has been demonstrated to be a superior coprological method for egg/oocyst recovery, especially for smaller GI parasite eggs, and more sensitive to low levels of *Trichuris spp.* and *Nematodirus spp.* when compared to other widely used methods such as simple standing flotation (Dryden, 2005) and McMaster techniques (Bello and Allen, 2009). Others have demonstrated that there is no significant difference between the two methods in detection of eggs of trichostrongyles (Howell et al., 2010).

Fecal samples were stored in a refrigerator or iced insulated cooler at 1–2 °C for 1–3 days and homogenized by mixing before being analyzed for GI parasite eggs/oocysts. We used approximately 5 g (range 4.8–5.2 g) of the homogenized sample for centrifuge separation using a modified centrifuge flotation method (Cox and Todd, 1962; Dryden, 2005). Through this method the homogenized sample was suspended in 20 ml of deionized water and strained through a tea strainer. The liquid portion was then divided equally into two 15 ml conical tube and spun in a swing-head centrifuge at 2000 rpm for 10 min. The supernatant was poured out of the conical tubes and 12 ml of Sheather's sugar flotation solution (specific gravity 1.27) (Dryden, 2005) was added to each test tube and the solid resuspended in the solution. The conical tubes were again spun in a swing-head centrifuge at 2000 rpm for 10 min. After spinning, the conical tubes were placed in a test tube rack and Sheather's sugar flotation solution was added until a reverse meniscus formed above the top of the conical tubes. A cover slip was placed on top of the conical tube for 30 min to allow for parasite eggs/oocysts to rise to the top of the solution and adhere to the cover slips. Both cover slips were then removed and placed onto a glass microscope slide. The slides were systematically examined in a grid pattern and eggs/oocysts of strongyle-type spp., *Nematodirus* spp., *Trichuris* spp., *Moniezia* spp., and *Eimeria* spp. were manually tallied under 10x magnification. The total count for both cover slips was then divided by weight (range 4.8–5.2 g) to a 1 g standard to account for slight variation for sample weight and recorded as the number of eggs/oocysts per gram (epg/opg) of the sample for each parasite type.

From May to September 2019 sub-samples of fecal collections were sent to UNL for multiplex polymerase chain reaction (PCR) testing to identify GI nematode species that may also be found in cattle, including *Ostertagia* spp., *Haemonchus placei*, *Oesophagostomum* spp., *Trichostrongylus columbriformis*, and *Cooperia oncophora*. DNA isolation from fecal eggs and the PCR were performed using primers and reaction conditions essentially as described by Zarlenga et al. (2001). The PCR test can identify GI nematodes using fecal eggs and primers that target various regions of the ribosomal DNA resulting in unique electrophoretic profiles for most major cattle genera. The test has a sensitivity of less than 0.5 egg-DNA equivalents per species. PCR fragmentation patterns were visualized by agarose gel electrophoresis and ethidium bromide staining. Size fragments defined in Zarlenga et al. (2001) were used as indicators of parasite genera.

2.3. Variables

For each sample collected, we recorded several variables to study the effects of demographics, management practices, location, and treatment effectiveness on bison FECs. For demographic differences in FECs, we recorded collection date, bison identity, sex, and age using the same counting method at both laboratories (CT and UNL). We also recorded metapopulation (North or South), herd size, pasture names, accessible grazing acres, and stocking rates to examine differences in egg/oocyst counts by grazing management practice and land use. Lastly, to examine the effectiveness of deworming treatments, we recorded if bison had or had not been treated with moxidectin or fenbendazole. For those bison that had been treated with either dewormer, we recorded the duration between the last treatment date and date that the fecal sample was collected. Full descriptions of variables derived from this data and used in analyses are presented in Appendix 1.

2.4. Statistical analyses

We compared FECs processed by UNL and CT using Welch two-sample t-tests and determined that the mean FECs of all strongyle-type spp., *Nematodirus* spp., *Trichuris* spp., *Moniezia* spp., and *Eimeria* spp. were collectively higher for samples processed by CT than by UNL (t = 6.67, p < 0.001). Differences in the average relative density of

Table 1
Physical description of each bison parcel, including total area, proportion of frequently and occasionally flooded soils (NRCS, 2020), and land use histories.

Parcel	Acres	Flooding Proportion	Land Use History
Visitor's Center	50	0% Frequent 0% Occasional	Reconstructed from an agricultural field in 2008.
Ruge-South Brown	387	0% Frequent 94% Occasional	Relict prairie, except for 48 acres reconstructed from an agricultural field in 1999.
North Meadow	177	7% Frequent 89% Occasional	Relict prairie.
Calving-Office Pasture	267	10% Frequent 86% Occasional	Restored from a woodland and exotic grass hay field, history of overgrazing by cattle.

Sheather's sugar solutions made in-house at each lab and used to process samples or potentially the size of test tubes used in differing centrifuge models may best explain the differences in abundance estimates between laboratories. However, the relative abundance of specific taxa was very similar between laboratories. Presenting summary statistics of pooled and unscaled raw data may reduce the influence of bias from either laboratory regarding measures of central tendency (Caudill, 2010). Therefore, we present summary statistics including mean and standard deviation of FECs by taxa for all age classes as well as median, quartile, and max FECs for taxa across the whole herd using pooled and unscaled raw. However, for modeling the influence of demographic, temporal, and treatment covariates on FEC estimates we accounted for the differences between processing labs via scaling variables by subtracting each observation by the respective sample mean, divided by the sample's standard deviation, then added each observation to the sample's minimum observed value plus 0.0001 for data processed at CT and UNL laboratories independently (Bring, 1994). Therefore, all observations were broadly equivalent to standard deviations above zero, with a minimum value of just above zero (0.0001). After scaling, there were no significant differences between samples based on processing laboratory (t = 0.98, p = 0.327), and therefore data were pooled for regression analyses. However, data remained positively skewed and overdispersed after scaling efforts and therefore we employed Gamma regression, which handles such distributions well, to model the influence of a suite of covariates on bison FECs (Fox, 2015).

Data were analyzed with Gamma family Generalized Linear Models with a log-link function using the stats package in R 3.6.0 (R Core Team, 2019). A total of 22 models were generated with the scaled sum of FEC as the outcome variable and a host of individual independent variables, which were all technically bivariate except for categorical and polynomial predictor variables (Appendix 1, Table 2). We organized predictor variables into four separate groups including spatial, demographic, temporal, and treatment covariates and compared models within each assemblage using Akaike Information Criterion (AICc) corrected for small sample sizes employing the 'model.sel' tool in the 'MuMIn' package in R (Burnham and Anderson, 2002; Barone et al., 2020; R Core Team, 2019). All model sets included a like null model regressing the dependent variable by 1. We considered all models with

an Akaike weight of 0.10 or higher as valuable predictor variables of fecal parasite abundance (Wagenmakers and Farrell, 2004).

3. Results

From 2015 to 2019 we collected and analyzed 293 samples (range = 17–134 samples/year) from 104 individual bison, opportunistically sampling individual animals from 1 to 11 times ($\bar{x} \pm SD = 2.8 \pm 1.9$). The CT lab processed 182 samples and UNL processed 111 samples. Total FECs ranged from 0 to 1451 epg/opg, with a median value of 27.5 epg/opg and a mean of 61.8 epg/opg (25th percentile = 9.4, 75th percentile = 72.5). Strongyle-type spp. were the most widespread and abundant eggs and were present in 95.2% of samples (median = 19.4 epg; $\bar{x}$ = 39.1; max = 392.7; Table 3). *Eimeria* spp. were present in 73% of the samples and were occasionally the dominant parasite by large margins in bison under one year of age but demonstrated wide variation in abundance (median = 1.4 opg; $\bar{x}$ = 15.3; max = 1451). *Moniezia* spp., *Trichuris* spp., and *Nematodirus* spp. FECs all demonstrated median values of zero and were present in less than half of the samples (41.6%, 30.7%, and 21.5% respectively). *Moniezia* spp. FECs were occasionally quite high (max = 292.1 epg) particularly during the first year of life, whereas *Trichuris* spp. and *Nematodirus* spp. FECs never exceeded 10 epg (max = 5.5 and 8.1, respectively). However, after scaling variables to the number of standard deviations above zero, it was clear that FECs of both *Trichuris* spp. and particularly *Nematodirus* spp. were much higher, on a relative basis, during the first year of a bison's life. This pattern was also true of *Moniezia* spp. and *Eimeria* spp. (Fig. 3). However, FECs of strongyle-type spp. appeared to peak during the second year of life (Fig. 3).

Variation in parasite epg/opg was apparent both between and within individual bison. Median scaled FECs ranged from near zero to over three standard deviations above zero for individual bison (Fig. 4). The interquartile range (IQR; gap between the 25th and 75th percentiles) of scaled FECs varied widely for individual bison, with some exhibiting a wide range (IQR > 2 SDs) and others demonstrating a narrow range over time (IQR < 0.1 SD; Fig. 4). The largest variation in IQR was observed in bison transitioning from a calf or yearling (0–2 years of age) to adolescence (greater than 2 years of age).

Table 2

Mean egg/oocyst counts per gram of fecal matter assessed by bison age class and discernible gastrointestinal parasite taxa.

Age Class Name	Age	Strongyle-type	Nematodirus	Trichuris	Moniezia	Eimeria	Total
New Calf $\bar{x}$ (n = 37)	0 ≤ 1	42.49	2.03	0.41	22.37	64.84	132.09
SD		67.62	2.50	0.98	54.18	240.13	250.15
F (n = 9)		26.01	1.31	0.11	15.53	58.29	101.23
M (n = 22)		48.65	2.74	0.61	26.25	14.38	92.58
Unknown (n = 6)		44.60	0.50	0.07	18.40	259.67	323.23
Yearling $\bar{x}$ (n = 52)	1 ≤ 2	60.08	0.26	0.11	10.29	17.69	88.42
SD		65.58	0.77	0.25	24.19	35.59	92.00
F (n = 28)		59.60	0.31	0.07	10.98	10.42	81.37
M (n = 24)		60.64	0.20	0.15	9.49	26.18	96.65
Juvenile-Adult $\bar{x}$ (n = 77)	2 ≤ 4	32.14	0.11	0.15	3.52	6.89	42.80
SD		51.74	0.42	0.28	11.36	15.53	57.47
F (n = 59)		38.05	0.15	0.15	4.18	6.67	49.18
M (n = 18)		12.74	0.00	0.12	1.37	7.64	21.88
Young-Adult $\bar{x}$ (n = 64)	4 ≤ 6	39.00	0.03	0.06	2.37	7.40	48.85
SD		53.22	0.08	0.16	5.76	17.66	63.66
F (n = 42)		48.72	0.02	0.08	2.61	8.33	59.76
M (n = 22)		20.44	0.04	0.03	1.91	5.62	28.03
Peak Adults $\bar{x}$ (n = 37)	6 ≤ 9	24.63	0.05	0.08	3.60	3.00	31.36
SD		32.95	0.26	0.19	9.46	10.79	38.18
F (n = 20)		21.00	0.00	0.05	0.31	3.71	25.06
M (n = 17)		28.90	0.11	0.11	7.47	2.17	38.76
Mature Adults $\bar{x}$ (n = 26)	9 +	34.27	0.03	0.07	3.16	2.07	39.60
SD		36.63	0.12	0.19	8.74	3.80	38.23
F (n = 22)		33.30	0.04	0.08	3.53	2.43	39.38
M (n = 4)		39.65	0.00	0.00	1.10	0.10	40.85
Herd $\bar{x}$ (n = 129)	0–13	39.14	0.35	0.13	6.83	15.32	61.76
SD		54.71	1.16	0.41	23.77	88.63	110.81

Table 3
Spatial, demographic, temporal, and treatment models of bison fecal parasite abundance ranked via Akaike Information Criterion, including covariate parameter estimates.

| Variable (fac. ref.)	Factor-Modifier	B	SE	t	p		df	LLV	AIC	delta	wt.
Spatial Covariates											
Pasture (Office-Calving)	North Meadow	−0.4276	0.2239	−1.91	0.057	^	5	−128.5	267.1	0.00	0.857
	Ruge-South Brown	−0.9317	0.3071	−3.03	0.003	**					
	Visitor's Center	−0.1871	0.2566	−0.73	0.467						
Density		0.1986	0.0955	2.08	0.038	*	3	−132.5	271.1	3.97	0.118
Stocking Rate		0.0433	0.0376	1.15	0.250		3	−134.7	275.5	8.37	0.013
Area		−0.0010	0.0010	−1.05	0.297		3	−135.2	276.5	9.38	0.008
Duration		0.0002	0.0004	0.39	0.700		3	−136.0	278.0	10.90	0.004
Null							2	−140.0	284.1	16.98	0.000
Abundance		0.0036	0.0033	1.10	0.270		3	−140.5	287.0	19.91	0.000
Demographic Covariates											
Age Class (New Calf 0 ≤ 1)	Yearling 1 ≤ 2	−0.3038	0.2970	−1.02	0.307		7	−114.2	242.9	0.0	0.990
	Juvenile-Adult 2 ≤ 4	−1.1719	0.2762	−4.24	0.000	***					
	Young-Adult 4 ≤ 6	−0.9633	0.2852	−3.38	0.001	***					
	Peak Adult 6 ≤ 9	−1.2468	0.3210	−3.88	0.000	***					
	Mature Adult 9 +	−1.3895	0.3534	−3.93	0.000	***					
Age-nearest integer		−0.1250	0.0284	−4.41	0.000	***	3	−123.3	252.7	9.82	0.007
Age-decimal year		−0.1225	0.0281	−4.36	0.000	***	3	−124.2	254.4	11.54	0.003
Sex (female)	Male	0.1338	0.1681	0.80	0.427		4	−132.5	273.1	30.23	0.000
	Unknown	1.4955	0.5714	2.62	0.009	**					
Null							2	−140.0	284.1	41.25	0.000
Herd (North)	South	−0.1200	0.2340	−0.51	0.608		3	−139.8	285.7	42.80	0.000
Temporal Covariates											
Year		0.3326	0.0748	−4.45	0.000	***	3	−129.0	264.0	0.00	1.000
Julian Data-polynomial	polynomial 1	1.4706	1.5220	0.97	0.335		4	−137.3	282.8	18.75	0.000
	polynomial 2	−2.3655	1.5220	−1.55	0.121						
Month- Polynomial	polynomial 1	1.8763	1.5335	1.22	0.222		4	−137.7	283.6	19.60	0.000
	polynomial 2	−1.8335	1.5335	−1.20	0.233						
Null							2	−140.0	284.1	20.12	0.000
Month		0.0340	0.0292	−3.12	0.245		3	−139.0	284.1	20.13	0.000
Julian Date		0.0009	0.0010	0.88	0.378		3	−139.5	285.0	21.00	0.000
Season (Fall)	Spring	0.2024	0.2938	0.69	0.491		5	−138.7	287.7	23.66	0.000
	Summer	0.2804	0.2354	1.19	0.235						
	Winter	0.1438	0.2582	0.56	0.578						
Treatment Covariates											
Fenbendazole Oral Deworm-time		0.0015	0.0002	5.89	0.000	***	3	−114.3	234.7	0.00	0.996
Fenbendazole Oral Deworm (Treated)	Untreated	1.0054	0.2123	4.74	0.000	***	3	−119.9	245.9	11.18	0.004
Moxidectin Pour-on Deworm-time		0.0009	0.0002	3.87	0.000	***	3	−128.5	263.1	28.43	0.000
Moxidectin Pour-on Deworm (Treated)	Untreated	0.6870	0.1886	3.64	0.000	***	3	−128.9	264.1	29.38	0.000
Null							2	−140.0	284.1	49.50	0.000
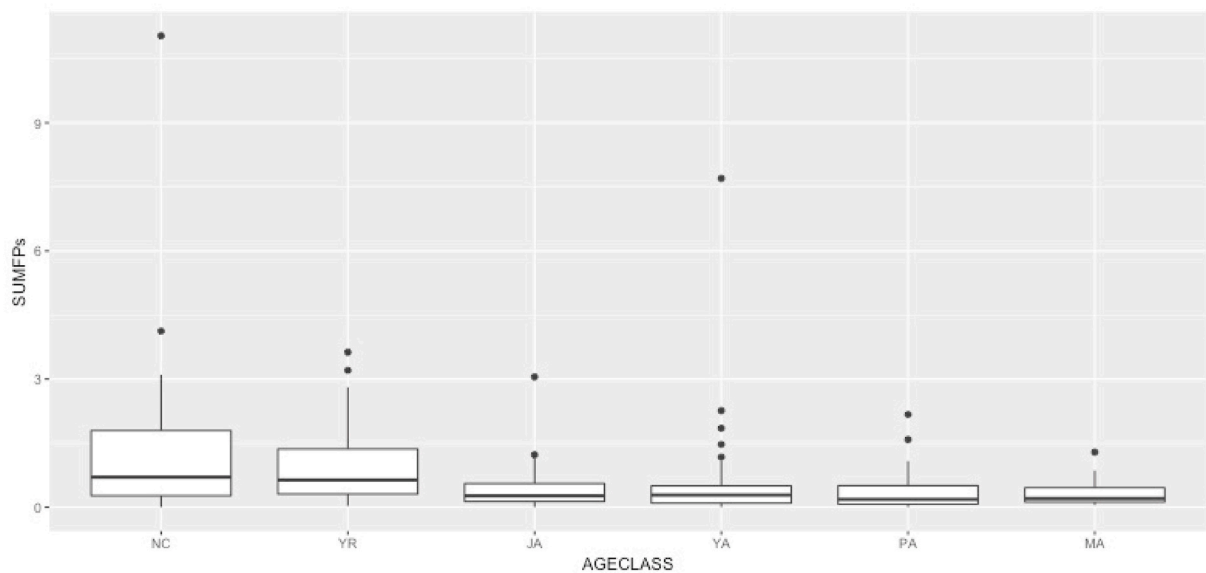
Fig. 2. The sum of FECs counted per gram of sample from bison of various age classes, including "NC" (New Calf; 0–1), "YR" (Yearling; 1–2), "JA" (Juvenile to Adult Transition; 2–4), "YA" (Young Adult; 4–6), "PA" (Peak Adult; 6–9), "MA" (Mature Adult; 9+). Black horizontal lines denote median values, while the top and bottom of boxes denote the upper and lower interquartile ranges (75th and 25th percentiles). Extending "whiskers" denote values of 1.5 times the interquartile range; points outside of this range constitute outliers.
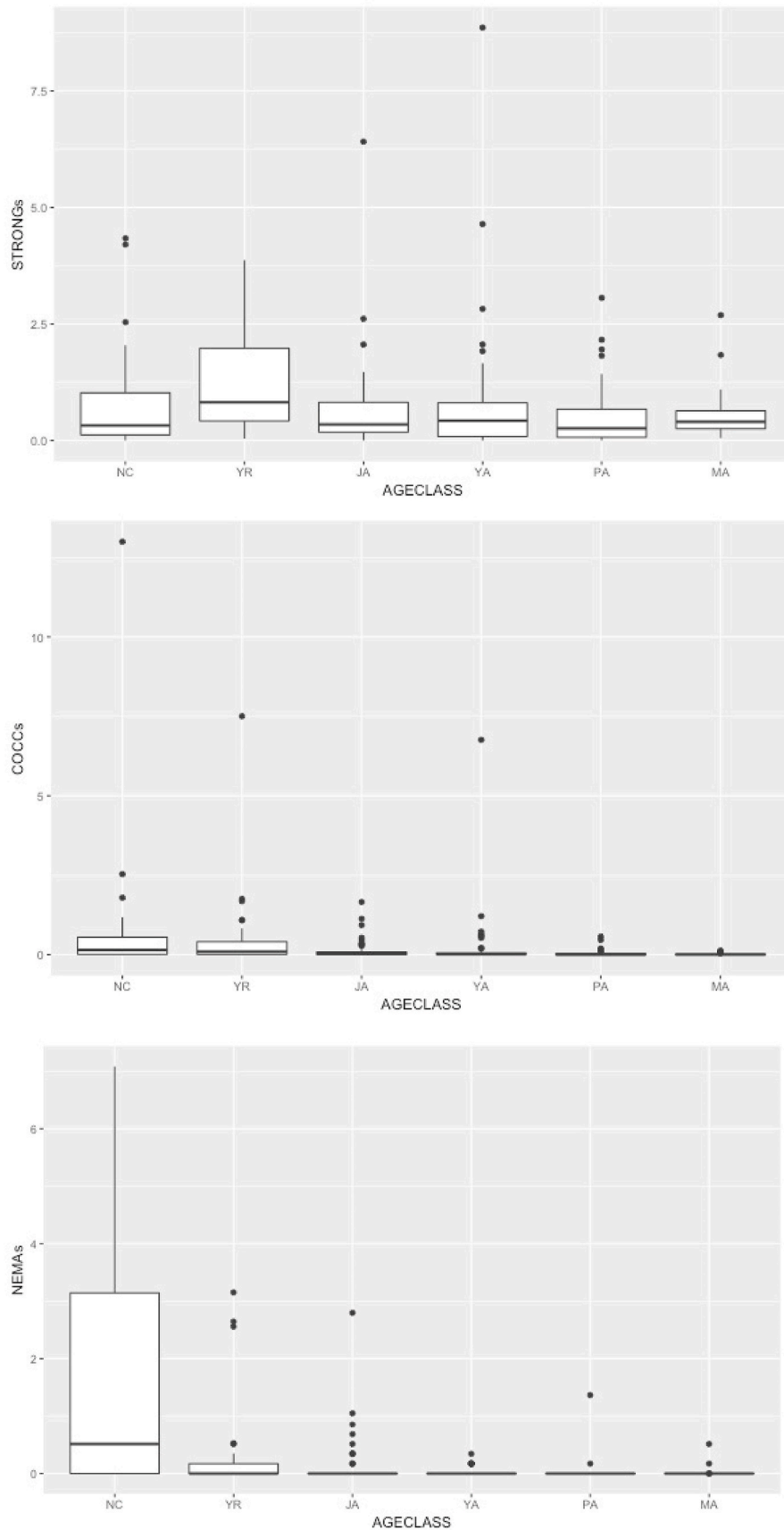
Fig. 3. The sum of FECs types, including "STRONGs" (Strongyle-type), "COCCs" (Coccidia), "NEMAs" (Nematodirus), "TRICHs" (Trichuris), "MONs" (Moniezia) counted per gram of sample from bison of various age classes. Ages classes included "NC" (New Calf; 0–1), "YR" (Yearling; 1–2), "JA" (Juvenile to Adult Transition; 2–4), "YA" (Young Adult; 4–6), "PA" (Peak Adult; 6–9), "MA" (Mature Adult; 9+). Black horizontal lines denote median values, while the top and bottom of boxes denote the upper and lower interquartile ranges (75th and 25th percentiles). Extending "whiskers" denote values of 1.5 times the interquartile range; points outside of this range constitute outliers.

Fig. 3. (*continued*).
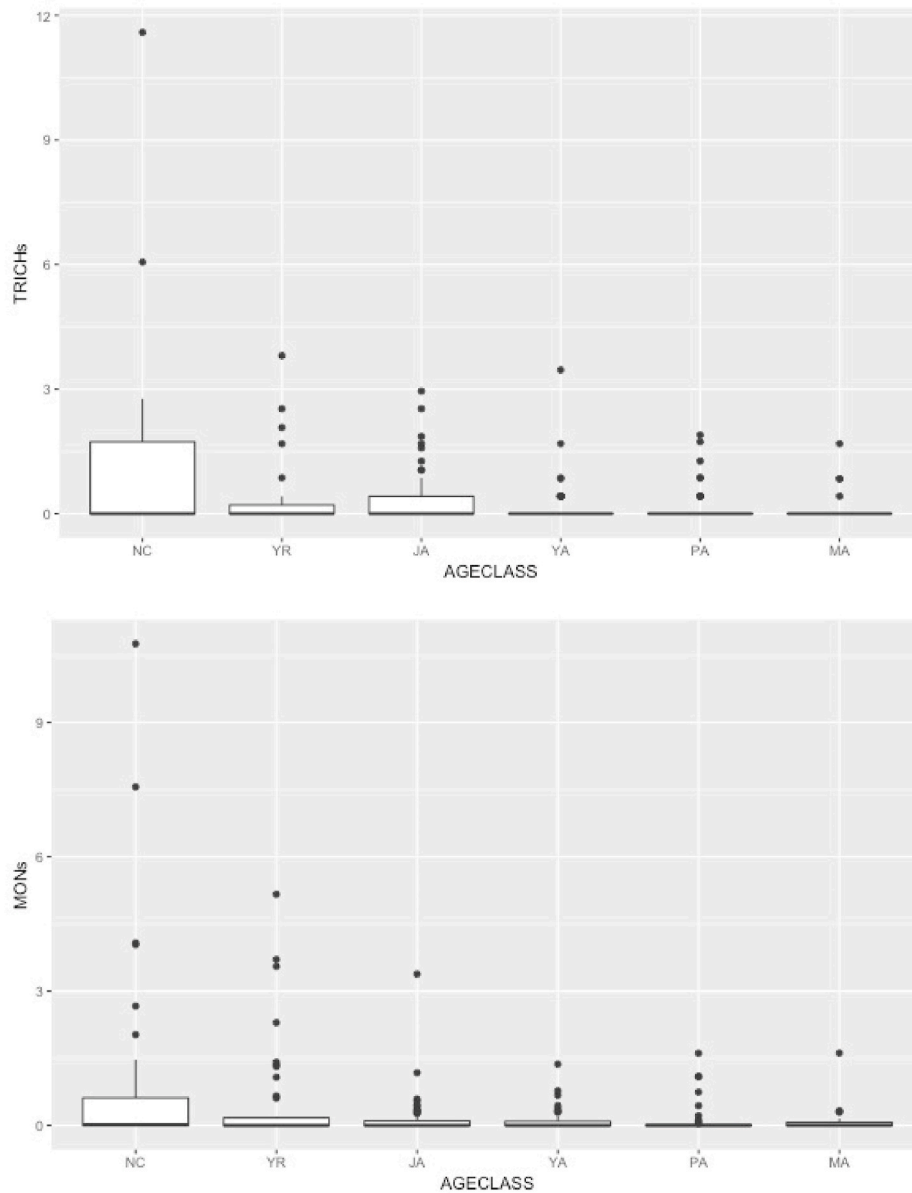
Our top performing demographic model was Age Class, which included five categories (Yearling 1 < 2, Juvenile-Adult 2 < 4, Young-Adult 4 < 6, Peak Adult 6 < 9, Mature Adult 9 +; AIC weight 0.990, Table 2). This model outperformed similar age variables, including age rounded to the nearest year and exact age in decimal years that were also significant (p < 0.001). Data indicated that the first two years of life are categorically distinct in terms of high FECs. Sex was not a significant predictor of total FEC, but the model outperformed the null model. Metapopulation (North or South) and grazing regime (rotational or continuous) were not predictive of FEC. Demographic findings suggest that calf and yearling (0–2 yrs age) bison have the highest FECs and that these decline as the age of the animal reaches peak adulthood and thereafter (x ≥ 6 yrs of age; Table 3, Fig. 2).

All spatial covariates outperformed the null model, with both the central access pasture and density of animals having a model weight of more than 0.10. Bison in the Calving-Office pasture had higher FECs than Ruge-South Brown and North Meadow (marginally) pastures but did not differ from the Visitor's Center paddock (Table 3). FECs increased with the density of bison, which interestingly outperformed stocking rate, which is a function of both density and duration. Only

three temporal covariates outperformed the null model, including year the sample was collected, the quadratic transformations (second order polynomial) of Julian date, as well as month of sample collection. Un-transformed month of the year and Julian date variables as well as season performed below the null model. However, only 'year' was a statistically significant (p < 0.001) or an important predictor (AICc model weight = 1.00) of FECs and demonstrated an increasing trend from 2015 to 2019 following bison reintroduction (Fig. 5).

Of the 293 samples processed, 57 were from bison not previously treated with fenbendazole and 87 were from bison not previously treated with moxidectin. All treatment variables outperformed the null model and were statistically significant from a hypothesis testing perspective (All models with *p* < 0.001; Table 3). Time since fenben-dazole treatment was the best predictor of FECs (AIC model weight = 0.996; Table 3) where FECs increased with time since the last treatment. Bison that had never been treated with fenbendazole had higher FECs than those that had been treated. Moxidectin treatments demonstrated similar, yet less robust effects. In both treatment cases there appeared to be a relatively long-term impact from a single deworming, but time since fenbendazole treatment clearly had the largest impact on FEC. The
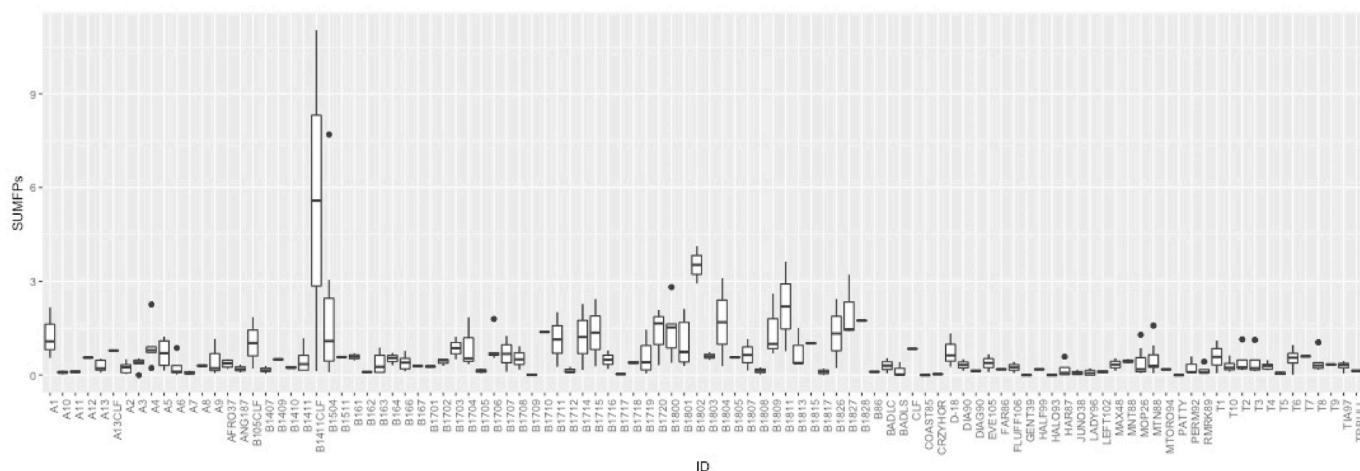
Fig. 4. The sum of FECs counted per gram of individual bison, demonstrating variation FECs between and among individuals. Black horizontal lines denote median values, while the top and bottom of boxes denote the upper and lower interquartile ranges (75th and 25th percentiles). Extending "whiskers" denote values of 1.5 times the interquartile range; points outside of this range constitute outliers.
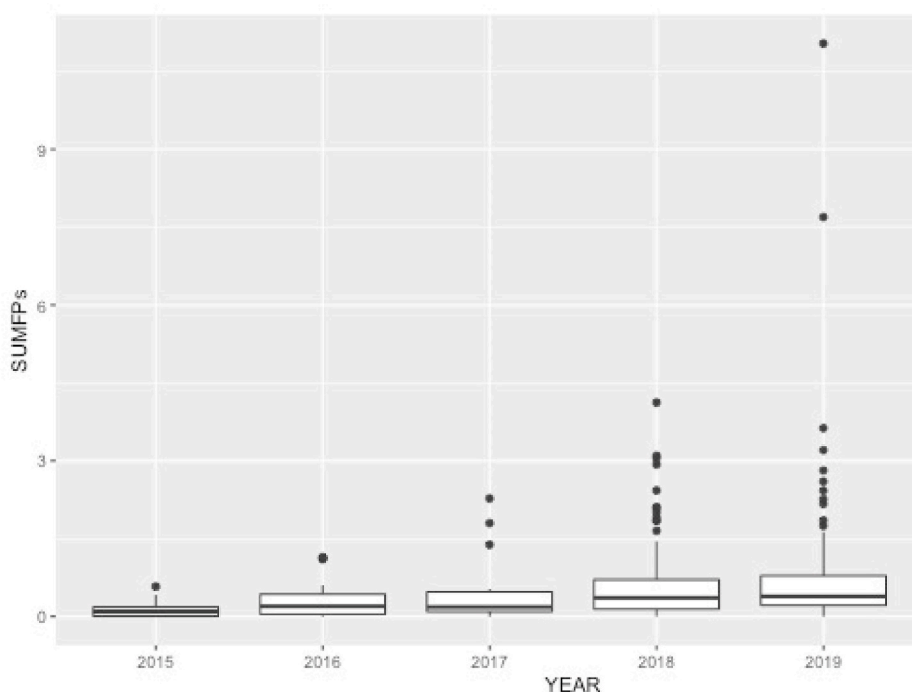

Fig. 5. The average sum of FECs counts by year, demonstrating and increasing trend in FECs between 2015 and 2019. Black horizontal lines denote median values, while the top and bottom of boxes denote the upper and lower interquartile ranges (75th and 25th percentiles). Extending "whiskers" denote values of 1.5 times the interquartile range; points outside of this range constitute outliers.

methods and results differ from a fecal egg count reduction test (FERCT), in that they are not testing the immediate response of anthelmintic treatment, but rather the long-term outcomes FEC of a treatment over extended periods of time.

Multiplex PCR assay of 28 bison samples revealed the presence *Ostertagia* spp. (93%), *Haemonchus placei* (93%), and *Cooperia onchophora* (89%) in both the North and the South metapopulations. However, only the smaller North metapopulation tested positive for *Oesophagostomum* spp. (10%). Neither metapopulation tested positive for *Trichostrongylus columbriformis* (0%).

4. Discussion

Although GI nematodes are thought to cause economic and clinical losses in bison, it has been unclear how demographics, management, land use history, and treatment influence the degree of infection (Dies and Coupland, 2001; Woodbury et al., 2014). Much of the data on GI nematodes of American bison comes from production and federal herds in the intermountain west and Canada, while information from Plains bison in a semi-wild setting within the Great Plains is lacking, despite being a major region of their historic and current range (Sanderson et al., 2008). Management plans for the ecological recovery of American bison and European bison as wildlife include promoting "wild" conditions and behaviors, such as providing unrestricted movement and the

processes of natural selection, while minimizing active management intervention (Pucek, 2004; Gates and Aune, 2010). However, a major reason managers regularly handle bison is to apply topical dewormer (USDA, 2016). Research indicates that clinically significant levels of GI nematodes that develop under conditions of restricted movement and high stocking densities can be effectively controlled with commercial anthelmintics (e.g., doramectin; Eljaki et al., 2016). Conversely, the use of anthelmintics to control GI nematodes may influence diet choice, grazing behavior, movement, limit natural selection by altering host immune profiles, and unintentionally promote domestication (Lehman et al., 2006; Gates and Aune, 2010; Stott, 2017). Our results suggest that young Plains bison (<2 years of age) are most at risk for clinically significant GI nematode infections, and that targeted drenching with fenbendazole have lower FEC thereby providing a competitive advantage to host immune systems (Kenyon et al., 2013). Our data also demonstrate that management practices of semi-wild bison herds, including animal density, affects FEC. Finally, our results indicate that pasture characteristics and long-term management histories may influence FECs and that Plains bison demonstrate significant overlap with cattle regarding GI nematode species and European bison (Knapp, 1993; Demiaszkiewicz et al., 2009, 2010). This is not surprising considering Plains bison at the Crane Trust were reintroduced to pastures previously grazed by cattle and that they currently graze in management units adjacent to cattle pastures. Holistically, our findings indicate that strategic management decisions such as resting pastures for extended time periods, maintaining lower animal densities, and strategic use of anthelmintics could help control GI nematode infections while limiting the need to frequently handle semi-wild bison herds.

The results of FECs by age, variation in FECs between and within individuals, and top performing demographic models all indicate that FECs peak within the first two years of age. This observation is consistent with other literature arguing that younger animals have less developed immune systems making them more susceptible to parasitic infections (e.g. Woolhouse, 1998; Cornell et al., 2008). As is noted in cattle and other semi-wild animal (i.e. reindeer) industries alike, bison likely develop natural immunities to GI nematodes as they age (Dineen, 1963; Waller, 2003; Kolodziej-Sobocińska et al., 2016), which is corroborated by our demographic model in which FECs were lowest after bison reached 6 years of age. Though some species such as *Ostertagia ostertagi* can escape the host immune system for extended periods of time (Klesius, 1993; Gasbarre et al., 2001).

Despite the high variation in FECs, mean FECs for this semi-wild Plains bison herd were like those reported in commercial bison in Canada (72 epg) (Avramenko et al., 2018). Like other studies (Dies and Coupland, 2001; Woodbury et al., 2014; Avramenko et al., 2018), strongyle-type infections were the most common in this bison herd. Prevalence of *Moniezia* spp. was slightly lower when compared to Dies and Coupland (2001) (54.6%) and considerably higher than found by Woodbury et al. (2014) (14%). When compared to other studies, *Trichuris* spp. prevalence was lower than found by Dies and Coupland (2001) (40.9%) and higher than found by Woodbury et al. (2014) (14%). Similarly, presence of *Nematodirus* spp. was lower than reported by Dies and Coupland (2001) (50%) and higher than reported by Woodbury et al. (2014) (14%). The presence of *Eimeria* spp. was lower than 97% as reported by Woodbury et al. (2014). Higher FECs of *Eimeria* spp. in Plains bison calves has been commonly reported in Montana (Penzhorn et al., 1994), indicating that infectivity of *Eimeria* spp. could be higher for calves than older bison. Ryff and Bergstrom (1975) propose that several *Eimeria* spp. are foreign parasites found within American bison that are indigenous to cattle, suggesting that bison may not as readily develop natural immunities to them. Similarly, Pyziel et al. (2019) demonstrated that *Eimeria* spp. are highly pathogenic and have been transferred from cattle to European bison. The FECs found in this study were of similar magnitude to that of relevant literature, indicating a broader application of our findings, including the conservation efforts of European bison. The FECs also suggests that GI nematode species in are

relatively similar across diverse landscapes, given our data mirrors those from different ecoregions (Woodbury et al., 2014; Penzhorn et al., 1994; Pyziel et al., 2018).

This study demonstrated that both moxidectin and fenbendazole had significant effects on the long-term FECs of Plains bison when testing the utility of at least one anthelmintic treatment in their lifetime. However, time since deworming with fenbendazole was the most significant treatment covariate. Our results suggest that ingested fenbendazole is more effective than pour-on moxidectin and likely other macrocyclic lactones at reducing FECs in Plains bison. This could be explained by treatment time, where fenbendazole was administered during the growing season when bison are more likely to acquire new parasites (Thomas et al., 2002). The low response seen from moxidectin may also be explained by timing of a pour-on moxidectin treatment, where bison were treated in the late fall when their coats are likely the thickest and may not reach the skin for absorption (Dies and Henderson, 1998). Moxidectin is generally applied during bison working periods, which increases the handling time and stress levels in bison. If pour-on moxidectin deworming treatments are indeed comparatively ineffective for bison, then eliminating the practice of administering this treatment may ultimately reduce working duration and reduce the risk of injury through elevated stress levels. Interestingly, a single oral fenbendazole or to a lesser degree pour-on moxidectin deworming treatment appeared to reduce epg/opg for subsequent years following treatment. In fact, the second-best treatment model after time since oral fenbendazole deworming treatment was whether individual bison had ever been treated with oral fenbendazole dewormer. Clearly, these treatments do not have such a prolonged direct impact. Fenbendazole, for instance, may control GI nematodes for only 4–6 weeks in conditions of repeat exposure following label recommendations. However, it is possible that reducing parasite levels when bison are young and vulnerable could provide their immune systems a competitive advantage against GI nematodes (Russell, 1949; Molento, 2009). Furthermore, research from livestock species suggest that more infrequent targeted anti-parasite treatments maintain treatment effectiveness over time better than label recommended whole herd treatments every 4 weeks (Molento, 2009; Kenyon et al., 2013). These results give insight into the real-world effectiveness of anthelmintics in a conservation setting, where treatment GI parasites may only occur opportunistically or once in a bison's life.

Our spatial models demonstrate that FECs varied highly between pastures. Despite being a pasture that was rested for short periods (less than 6 months) from bison grazing through rotation, FECs in bison in the Calving-Office pasture seemed to produce the highest FECs. This may be explained by a land use history of continuously high cattle stocking rates with no periods of rest in a 10-year period of rest prior to being converted to a bison pasture. Another possible explanation is cross-species transmission of parasites from wildlife (Walker and Morgan, 2014; Miller et al., 2017) like deer, which have been seen abundantly in this pasture (Brice Krohn, pers. comm., October 2020). Calving-Office pasture also contained a greater proportion of frequently flooded area (NRCS, 2020; Table 1) than the other pastures which are more upland and well drained. High moisture levels and finer soil texture are noted to retain oocysts more readily which may correlate with higher FECs in ruminants (Walker et al., 2001; Sohail et al., 2019), this could indicate that bison become more susceptible to higher FECs when present in wetter habitat types or in historically overgrazed pastures. High stocking density correlated with higher FECs; however, rotational grazing and lower stocking rates which traditionally reduce parasite burdens in ruminants (Thamsborg et al., 1996; Berezowski et al., 2018), were not predictors of low FECs by our models. This suggests that overall density (Arneberg et al., 1998) was the key driving force for controlling FEC and possibly worms burdens. Stocking density also explains temporal variation inasmuch as herd population increased every year during the study. However, our study did not account for temporal variations in climatic or moisture conditions which could be contributing factors as well (Sohail et al., 2019). Interestingly, the smaller North

metapopulation at the Visitor's Center pasture had similarly lower FECs to the higher quality remnant prairies, despite being continuously grazed with a high stocking density by bison. This may have been associated with a land use history of being an agricultural field reconstructed to a tallgrass prairie before bison were introduced (Table 1).

PCR analysis of strongyle-type parasites revealed that Plains bison share some of the same species of parasites as cattle and European bison (Knapp, 1993; Demiaszkiewicz et al., 2009, 2010; Pyziel et al., 2018). Since much of bison veterinary science is limited to applying cattle-based knowledge, understanding which parasite species are shared between cattle and bison may help managers derive better information to how to effectively combat parasites, which is important in recognizing which parasites may pose the most significant threats to bison. The generalist nature of GI nematodes makes cross-species transmission a common occurrence, though research on cross-species transmission of parasites between wild and domestic ungulates is limited (Walker and Morgan, 2014; Barone et al., 2020). Furthermore, there are about 1800 private U.S. ranches and farms raising bison (Carter and Matheson, 2017) and most are smaller producers. Among these, the total U.S. herd population is about 375,000 with an additional 125,000 in Canada. However, only about 30–50,000 are pure North American bison mostly on federal lands; while the balance are bison/-cattle hybrids. This offers further support for the crossover of cattle GI nematodes to the greatest population of bison (i.e., bison-cattle hybrids in the U.S.). Several studies note the most common shared genera between cattle and both American and European bison include *Oesophagostomum* sp., *Cooperia* sp., *Haemonchus* sp., *Ostertagia* sp., and *Trichostrongylus* sp. (Eljaki et al., 2016; Avramenko et al., 2018; Pyziel et al., 2018). Recently, widespread resistance has emerged to benzimidazoles (the active ingredient in fenbendazole) within GI nematodes of bison herds across North America and Europe has been reported (Pyziel et al., 2018; Avramenko et al., 2020). In order to reduce the risk of interspecific transfer of resistant parasitic strains, it may be important to maintain spatial distance between bison and cattle when grazing practices employ both species. Likewise, a temporal resting period between switching from cattle to bison reintroduction in parcels should also be considered to mitigate the risk of parasitic transfer.

The similarities between American and European bison reintroduction, management, and GI parasite composition indicate that this study may have wider implications beyond Plains bison herds, and the results could be used to better understand demographic and regional variation in GI parasites and to develop mitigation strategies in recovery efforts for both species. Our data suggest that FECs of GI nematodes spike in the first two years of a Plains bison's life. Reducing herd-level treatment to younger animals only, may reduce the abundance of GI nematodes on pasture while also reducing drug residues in the animals and on pasture and reducing the presence of resistant genotypes by maintaining refugia. Therefore, routine surveillance is critical. Newly introduced bison in Europe and North America should be screened and if necessary, treated for GI nematodes to prevent translocation of foreign parasites into the herd. Administering an oral application of fenbendazole may be an effective strategy to reduce GI nematodes in bison when high FECs are detected. Adopting a prescription-only or demographically targeted treatment practice could help bison naturally develop immunities to GI nematodes and avoid the worst parasite outbreaks, while reducing the risk of treatment resistance and handling. Future research should focus on the effectiveness of administering a one-time anthelminthic treatment to younger calves, which may reduce initial risks of high FECs, while still allowing for natural immunity development. Exploring new ways to administer parasite treatments, such as a direct oral treatment during working periods or injection, to younger bison may be beneficial to ensure that treatments are more demographically targeted and reduce the risk of only dominant adults ingesting medications. Further examination of parcel grazing during wet periods or more frequent rotation between bison pastures may also be warranted to mitigate the risk of high FECs.

Acknowledgements

APPENDIX 1. Narrative descriptions of independent variables utilized for statistical analyses

Variable	Description
Julian Date	Julian date (day of the calendar year 1–365 (366) that fecal samples were collected from the bison
Month	Month of the year fecal samples were collected from the bison
Season	Season (Spring: Mar.–May; Summer: June–July; Fall: Sept.–Oct.; Winter: Dec.–Feb.) fecal samples were collected
Source	What lab conducted fecal egg/oocyst counts: the Crane Trust (CT) or the University of Nebraska-Lincoln School of Veterinary Medicine (UNL)
ID	Standardized-unique animal ID: Contains ear tag color (i.e.-"B" = "Black") followed by tag number. In case of removed tag, contains shortened name "Mountainous" = "MTN" followed by former ear tag number – i.e.- "MTN88". Calf pre-ear tag number = mother's ear tag number followed by "CALF", i.e.- "B105CALF"
Sex	Coded as "M" for male and "F" for female
Age-decimal year	Years since birth
Age Class	Ordinal groupings of bison by "age classes" reflective of the natural breaks in Bison development = New Calf (NC; 0–1), Yearling (YR; 1–2), Juvenile to Adult Transition (JA; 2–4), Young Adult (YA; 4–6), Peak Adult (PA; 6–9), Mature Adult (MA; 9+).
Age-integer	Age rounded to the nearest whole year
Herd	North (N) or South (S) metapopulation
Strongyle	Blood worm eggs per gram feces
Nematodirus	Roundworm eggs per gram feces
Trichuris	Whipworm eggs per gram feces
Moniezia	Tapeworm eggs per gram feces
Eimeria	Intracellular parasite oocysts per gram feces
Total Fecal Parasites	The sum of all eggs/oocyst counted of strongyle-type, *Nematodirus spp.*, *Trichuris spp.*, *Moniezia spp.*, and *Eimeria spp.*
Herd Size	Number of animals in the herd
Oral Fenbendazole Dewormer-time	Number of days since oral de-wormer feed was put out. Time since treatment capped at 3 years (1095 days) just beyond the combined max value from time since pour over and time since tub treatment (1057)
Pour-on Moxidectin Dewormer-time	Number of days since de-wormer topically applied during bison working. Time since treatment capped at 3 years (1095 days) just beyond the combined max value from time since pour over and time since tub treatment (1057)

(continued on next page)

(*continued*)

Variable	Description
Pasture	"Central Access Pasture" or management unit to which bison had access
Size	Number of acres in Pasture
Duration	Number of days confined to CAP
Stocking Rate	Animal Unit Months per Acre
Density	Animal Units per Acre

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