

Dear Dr. Merbold,

Please find attached the responses to Referees and changes that were made to bg-2020-38, "Methane efflux from an American bison herd". We comprehensively revised the manuscript and added an independent footprint analysis following Kljun et al. (2015). The contributions of Natascha Kjlun warranted coauthorship and we included her in the revised version, which we agree is much improved as a result of her help and the Referee comments. We thank you for your support of the manuscript and we are happy to provide any additional information.

Sincerely,

A handwritten signature in black ink, appearing to read 'P. C. Stoy', written in a cursive style.

Paul C. Stoy
University of Wisconsin – Madison

Anonymous Referee #1

Received and published: 21 March 2020

GENERAL COMMENTS:

In this paper, Stoy et al. estimate bison enteric emission using the eddy-covariance method, coupled with a footprint model and a cattle location method. This type of approach is under development (Felber et al., 2015; Coates et al., 2017; Dumortier et al., 2017; Prajati et al., 2018; ... all cited in the document) and has the advantages of providing an estimate in the field, integrating the animal to animal variability, having great temporal resolution and the potential to be automated. The current bison herd is small but growing and the application of such a method is especially interesting on a wild species on which the classical methods by metabolic chamber or on-animal tracers are undoubtedly more complicated to apply. Therefore the scientific interest of the paper is proven. However, this method faces technical and methodological difficulties that limit its accuracy. The choice and accuracy of the footprint model, the technical difficulty of automatic tracking of livestock location, the best way to calculate a turbulent flux in non-stationary conditions, and the best way to determine a flux per individual based on turbulent flux and contribution to the footprint are still insufficiently investigated.

However, the paper does not present any significant advances on these points. Geo- location is carried out by manual analysis of images in the visible range, resulting in a restricted dataset of about 170 half hours, making it impossible to study a seasonal or even diurnal evolution of the emissions, a footprint model is arbitrarily chosen and is not compared to other available models and the difficulties related to non-stationarity are not addressed. The paper traces its path, in a pragmatic way admittedly, relying on choices made by other authors and not yet consolidated. An analysis of the dependence of flux on u^* in the absence of bison is proposed, with the aim of identifying a possible filtering criterion for low turbulence, but it is inconclusive in my opinion because of the low magnitude of the fluxes, both of CH₄ and CO₂. So there is little methodological input. A positive point from this point of view is the sensitivity analysis of the estimation of flux per individual to the precision of geolocation/precision of the footprint model. Some parts are however difficult to follow (e.g. smoothing of positions, see note below).

Some parts of the paper don't seem very useful to me. I am thinking in particular of the justification for the fact that the methane emissions measured do come from livestock (low background flux, i.e. from the soil/plant continuum). This is an essential part of the method, but it seems quite obvious to me for an ecosystem of this type in the winter conditions encountered. The observation of the absence of CH₄ flux when the bison are removed from the pasture seems to me sufficiently meaningful and I don't see the point of presenting the absence of dependence of the CH₄ flux on abiotic variables (radiation, temperature) to substantiate this observation. I was also hampered by some speculative passages (e.g. mechanisms of flux dependencies to u^* , role of excreta, possible diurnal variability) and the perspectives are certainly well written but already known by the community.

Remains the main message that, despite the large uncertainties in the enteric emission per individual, the enteric flux is lower than that of other types of ruminants. It is stated in the introduction that since bison have a grazing behavior that favors nutrient-rich species they may have lower enteric emissions

but in this study fodder is provided and is not characterized precisely, neither in terms of quantity nor in terms of quality. The reader therefore has no leads to circumstantiate this result.

I therefore feel that this article is premature and that the critical mass of original and useful information for the community is not reached at this stage. I encourage the authors to expand their dataset to allow for a statistically robust analysis of the quality of the footprint model, of the diurnal flux variability, to investigate methodological limitations in more detail and to propose explanations for low bison enteric emissions. Because I think the topic deserves a new and more robust submission when the above comments will be addressed, I also added below my specific comments, hoping it will help the authors to improve their analysis.

I would also like to point out that the shape of the paper is good, the writing is fluent, the references appropriate and the figures clear.

We largely disagree with this assessment but thank the Referee for the kind notes about the writing of the manuscript. We were generously allowed to measure animals from a privately-owned herd during a select period of the calendar year and did so to the best of our abilities under the reasonable condition that disturbance to the herd be minimized, hence the automated camera approach and three-month sampling period. The method to determine average bison contribution outlined in equations 1-3 is novel and builds upon previous work demonstrating that point- or near point-sources can be captured effectively using eddy covariance (Dumortier et al., 2019; Prajapati and Santos, 2019). The diurnal evolution of the flux estimates was investigated and found not to be significant. We are puzzled that our manuscript, which to our knowledge makes the first measurements of the methane emissions of non-domesticated ruminants, was insufficiently novel. It seems like the caution with which we are interpreting our measurements – for example, exploring u^ dependencies and methane efflux in the absence of bison – are being mistaken for a lack of novelty. We note that background emissions are a major source of uncertainty of the seasonal course of methane measurements from feedlot studies of cattle (e.g. Prajapati and Santos, 2019) and felt that it was important to study this.*

That being said, we made numerous changes to the manuscript to further improve it. We added the Kljun et al. footprint model as an independent estimate of the footprint with the generous assistance of Natascha Kljun who we added as a coauthor and also added detail about the magnitude of the corrections as noted below; thank you for suggesting that we do so. We comprehensively revised the manuscript in response to reviewer comments and feel that the revision represents a marked improvement.

L20: The uncertainty of 14 gCH₄ day⁻¹ bison⁻¹ mentioned in the abstract without any additional comment is, as clearly explained in L194, only including spatial uncertainty (and I have some concerns on this point, see below) and uncertainty due to the flux summation. Information on the huge dispersion on your $\langle f \rangle$ estimates (standard deviation of 61 gCH₄ day⁻¹ bison⁻¹ !) is not even mentioned in the abstract, which is misleading.

Uncertainty was calculated by summing the uncertainty due to spatial location and adding flux measurement uncertainty. The half-hourly uncertainty mostly averages out in the daily sum; consider for example a time series of half-hourly carbon dioxide flux data of an ecosystem during the growing season that follows the expected pattern with light. Taking the average value over the course of a day will have a large standard error but each individual measurement is accurate to within the accuracy of the flux measurement.

L28-70: Nice introduction.

Thank you, we wanted to describe why such measurements are necessary, especially in light of the ongoing success story of bison reintroduction in the North American Great Plains for which we owe a debt of gratitude to Tribal Nations in the US and First Nations in Canada.

L78: The composition of the herd is not specified. Age distribution could strongly influence CH4 emissions.

Thank you for pointing this out; we asked the landowners for the age distribution of the animals and they graciously agreed with a comprehensive table that included sex, weight, and more. We plan on adding a revised version of the table below to a new Supplemental Information section. We also added text to the discussion and a new reference noting the importance of animal age (and especially size) on per-animal methane efflux. Information from the landowner also clarified a question that we had about the number of animals in the pasture. Staff had originally told us that there were 40 animals but records indicate 39, which aligns better with the numbers from counts. We adjusted our location maps accordingly and re-ran the analyses.

SEX	BIRTH YEAR	WEIGHT (lbs.)	Weight (kg)	WEIGHT DATE	PREGNANCY STATUS
F	2010	1030	467	11/16/17	Y
F	2010	924	419	11/16/17	Y
F	2010	944	428	11/16/17	Y
F	2010	1055	479	11/16/17	Y
F	2010	1125	510	11/16/17	Y
F	2010	1050	476	11/16/17	Y
F	2010	1085	492	11/16/17	Y
F	2010	1000	454	11/16/17	Y
F	2010	1250	567	11/16/17	Y
F	2010	1050	476	11/16/17	Y
F	2010	1095	497	11/16/17	Y
F	2010	1015	460	11/16/17	Y

F	2010	976	443	11/16/17	Y
F	2010	958	435	11/16/17	Y
F	2010	940	426	11/16/17	Y
F	2010	1050	476	11/16/17	Y
F	2010	906	411	11/16/17	Y
M	2012	1425	646	11/16/17	
M	2012	1545	701	11/16/17	
F	2014	840	381	11/16/17	Y
F	2014	904	410	11/16/17	Y
F	2016	736	334	11/16/17	
F	2017	242	110	11/16/17	
F	2017	318	144	11/16/17	
M	2017	353	160	11/16/17	
F	2017	367	166	11/16/17	
M	2017	305	138	11/16/17	
M	2017	335	152	11/16/17	
M	2017	325	147	11/16/17	
M	2017	403	183	11/16/17	
F	2017	212	96	11/16/17	
M	2017	458	208	11/16/17	
M	2017	230	104	11/16/17	
M	2017	360	163	11/16/17	
F	2017	279	127	11/16/17	
M	2017	299	136	11/16/17	
M	2017	364	165	11/16/17	
M	2017	278	126	11/16/17	
F	2017	279	127	11/16/17	

L118: One or two additional lines on spectral corrections would be useful. Lateral separation, reference cospectrum, magnitude of the correction factor.

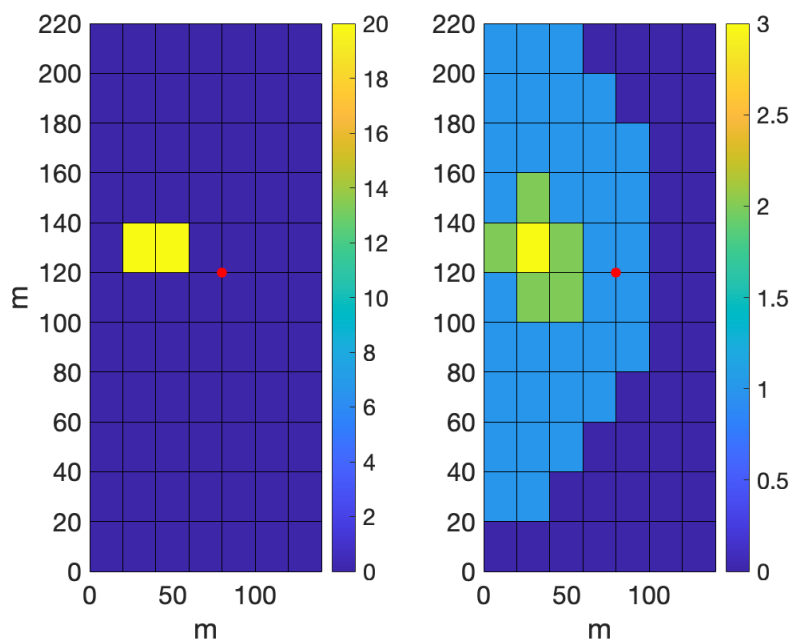
We added information about the magnitude of the correction factors to CH₄ fluxes (on the order of 14% when bison were present) and now note the LI-7700 which was offset in the horizontal by 22 cm (which is less than the dimensions of the optical path of the instrument at 50 cm) and 0 cm in the vertical.

L146-147: Too little information is given on the visual geolocation of bison based on the cameras. All we know is the position of the cameras and "manually attributing bison locations to squares in a 20m

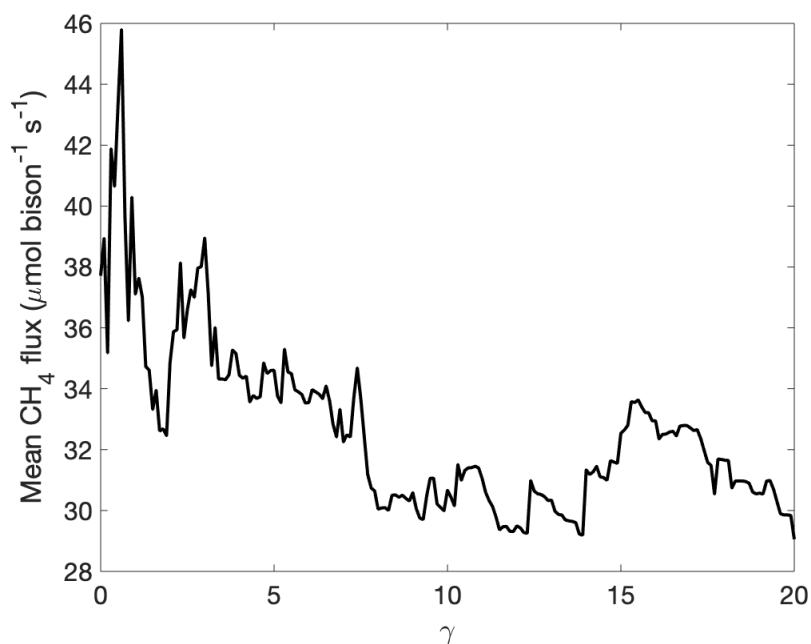
grid". How can you assign a distance to the mast with cameras that have no high-angle views and no distance markers in the different azimuths? Are the images from the different cameras combined to triangulate the positions of each individual? And how are the 6 positions averaged at half an hour? The authors propose an uncertainty of 20m on this estimate, which seems small in the absence of details on how to proceed.

Features in the field made it reasonably easy to determine locations (with uncertainty) and we took averages of the six positions for the half-hourly location estimates. Because these and all measurements have uncertainty we decided that it would be appropriate to perform the sensitivity analyses on locations to ensure that our uncertainty is not underestimated. We are more interested here in correctly characterizing uncertainty than pretending that our eddy covariance measurements of non-domesticated ruminants in wintertime in Montana have low uncertainty.

The bison location work has an interesting caveat. It makes little difference to the flux calculation. Take for example an extremely conservative viewpoint of bison location that assumes almost no ability to attribute bison to a particular location outside of a general location on one side of the tower. Such a situation is demonstrated on the right-hand side of the figure below where the Lagrange multiplier is set to 20 for a bison location estimate that happens to be from Jan. 22 at 11 am when bison were clustered in a clump, shown in the subplot below on the left, which is pretty easy to observe (see for example Figure 2 in the manuscript).



If we extend the Tikhonov Regularization analysis to a Lagrange multiplier of 20, representing a very crude visual guess as to the bison location as demonstrated above, the average per-bison methane flux value over the measurement period is about $30 \mu\text{mol CH}_4 \text{ bison}^{-1} \text{ s}^{-1}$ as demonstrated below. This is admittedly much smaller than the derived estimate of about $38 \mu\text{mol CH}_4 \text{ bison}^{-1} \text{ s}^{-1}$, but we also feel that we can place bison on the landscape using 8 cameras much more accurately than such a wild guess. That being said, the location attribution approach results in uncertainty, and our sensitivity analyses is designed to characterize this uncertainty. Despite this we engaged in the independent footprint estimates as suggested. Initial results are promising and helped us further characterize the uncertainty in our observations.



We undertook the rather comprehensive spatial uncertainty estimates because we were fully aware that the measurements had uncertainty and we sought to be exceedingly honest about the uncertainty in per-animal flux measurements that resulted. Such honesty should not be interpreted as lack of rigor.

L151-155: The paper is not self-standing on the point of "2D Tikhonov regularization". More information is needed so that the reader can understand the concept without having to read the reference assiduously. I do not master this technique but when I see that this spatial smoothing results in redistributing 3 individuals from the group at (x=40-80m,y=80-100m) to a distant group on the example of fig 4, I wonder about its relevance to simulate possible errors of location or footprint function.

We revised section 2.6 to further describe Tikhonov regularization approach used to interpret the bison location estimate with caution. To be honest we were delighted that regularization had the effect of redistributing individuals to different groups (this is entirely due to rounding to full integers), which we felt shared similarities to the tendency of animals to move between different groups as part of their social behavior.

L142: The approach used to determine $\langle f \rangle$ gives an estimate per half hour. However, the half hours with low contribution to the footprint will show a large dispersion, as this term is used in the denominator in eq. 3. Did the authors try to determine $\langle f \rangle$ rather by flux regression vs. contribution to the footprint?

We did not determine $\langle f \rangle$ by flux regression in the manuscript as we believe that this would not fully incorporate the dynamic that exists between bison locations and the flux footprint. (More directly, we feel that it is incorrect to do so and are surprised at this suggestion.) An earlier effort to estimate CH₄ flux as a function of bison count estimated the effective number of bison in the footprint but the regression was poorly constrained and subsequent work improved the flux footprint location. Instead – and admittedly we should have been clear about this in the original manuscript – we thresholded the dataset to exclude per-animal flux values using outlier identification which we subsequently revised now describe in more detail in the revised manuscript.

L148-150: I don't think that shifting everything by 1 grid-square cell in each cardinal direction can simulate a systematic error of the footprint model. Proceeding in this way, the impact on the estimation of the mean of the half-hourly $\langle f \rangle$ will be smoothed. I would understand better if it was systematically shifted by 1 grid-square farther/closer with respect to the mast (modify r in polar coordinates).

We somewhat disagree, because in our case this is equivalent to shifting the bison distribution in the opposite direction. But we do agree that the inference is reversed in this case and that the flux footprint location likely has less spatial bias than the bison count estimation. We re-analyzed the data by shifting the bison location estimates rather than the flux footprint location estimates; thank you for the suggestion.

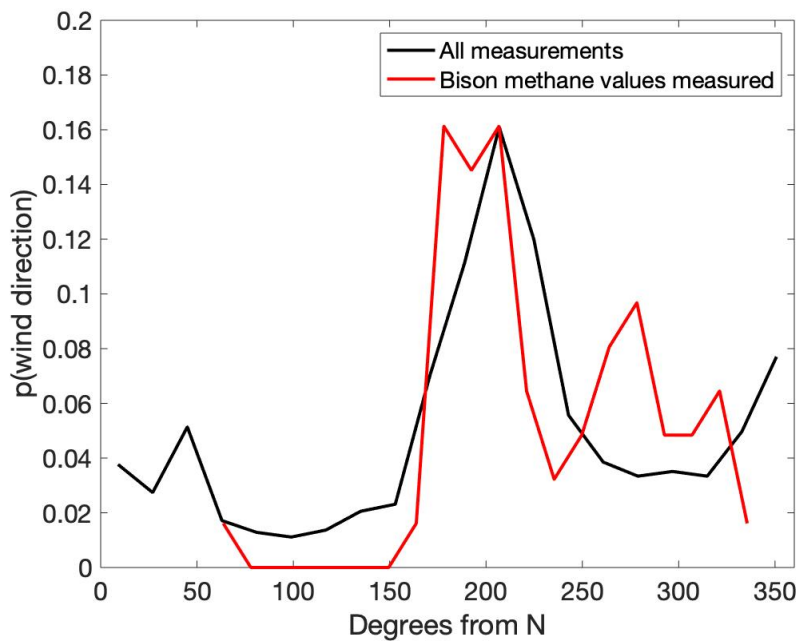
L184-187: It is not clear whether Fig. 10 only shows the locations for the 173 half-hourly periods where CH₄ fluxes are also available or whether it is the 444 half-hourly periods with camera tracking. The first option seems less misleading to me.

We did not intend to be misleading; rather we wanted to demonstrate the diurnal behavior of the bison to demonstrate to the reader that they usually congregate in directions upwind of the tower. We re-created the figure to only include observations for which fluxes were measured.

L184-187: The forage was not brought in the direction of the prevailing winds. As a result, cattle are often on the sides of the footprint. Is Hsieh's model reliable under these conditions? You suggest that the analytical models were validated for this type of exercise (L249) but it was not the Hsieh model.

The forage was delivered by employees of the private ranch due west of the tower in a place where the field was accessible from the road. Wind most commonly arrived from the southwest, but there is a secondary peak of wind directions from due west during periods when methane measurements were made (see below). Bison tended to congregate to the south, southwest, and west of the tower such that

there was considerable overlap between bison and the flux footprint. We were fortunate in this regard because we placed the tower in the center of the field (Figures 1 and 3) as we felt that it was the best practice for flux measurements and bison tended to congregate in the dominant wind directions, noting that the footprint can be rather broad due to the variance of the lateral wind velocity as demonstrated in Figure 3. To further extend the sensitivity analysis on the flux calculations, we added the Kljun et al. model to the analysis as an independent and additional assessment of the results.



L196: You should explain how you combine the spatial uncertainty and the uncertainty due to long-term methane flux sums (but annual sums in Deventer et al., 2019, what is the logic behind using it here?)

We combined uncertainty values by summing variances then computing the standard deviation.

L204: The Hogan's publication is 17 years old already. You should rely on more recent literature. Also, the 60 kgCH₄ per year per animal for range cattle is an average over very contrasted cattle nature. It would be useful to be more precise.

Older values are not necessarily less reliable but we added newer references including Prajapati and Santos, 2019, which was published as we were preparing the manuscript and escaped our initial notice, thank you for the suggestion.

L238-241: not convinced by the statistical reliability of this assertion. Since it seems to be the case for you too, Figure 13 should be removed.

We spent quite a bit of time trying to interpret if methane efflux differed over the course of the day as a function of their preferred feeding times but results were not conclusive. We removed Fig. 13 and now simply note in the text that significant diurnal methane flux patterns were not observed.

Fig 5: Is it really necessary to show (and use in statistical analyses) both SW and Rnet?

From the observations these variables differ rather strongly due in large part to the brightness of the snow and the differences between the snow surface temperature and sky temperature in the longwave. That being said, we do not use net radiation in subsequent analyses and removed the subplot to make the figure less busy.

TECHNICAL CORRECTIONS:

L191-193: the range 36-44 is repeated twice. Probably a typo?

Thank you for pointing this out. We looked into it and it happens that both approaches independently arrived at the same range. We assume that this is due to chance.

L196: gCH4 bison-1 day-1 instead of gCH4 m-2 day-1 !!!

This is correct, thank you for pointing out this error.

L211: 'negative' instead of 'positive'

Referee #2 also noted this error and it is now corrected, thank you for the careful read.

L494: something is wrong in this sentence.

The sentence was unnecessarily wordy. We re-wrote it to state 'Figure 3: An eddy covariance flux footprint calculated following Hsieh et al. (2000) and Detto and Katul (2006) at 1 m resolution for a single 30-minute interval superimposed on the study field (Figure 1).'

Fig 6: For better readability, the tower should be the origin of the spatial scale. Also in fig 10.

This is an interesting point and we carefully considered it but decided to keep the figure as is because it aligns with the grid in Figures 1 and 3 that we used to attribute bison locations. We did change the font size of the figure to have more information along the x-axis.

Fig 7: add ticks for the x scale.

We agree that tick marks on the x axis are an improvement and added these along with standard error bars as recommended by Referee #2.

Fig 9: ustar should be in m s⁻¹

Our apologies, this is clearly a typo on our part. The figure has been revised.

Review for “Methane efflux from an American bison herd”

General comments

The manuscript “Methane efflux from an American bison herd” from Stoy et al. presents winter CH₄ fluxes from a bison grazing system combined with a flux footprint analysis to estimate average CH₄ fluxes per animal and day. It addresses the interesting scientific question on the magnitude of bison emissions. The data is presented in a clear structure and easy-to-follow writing style. The manuscript uses methods which have been shown with varying success elsewhere (e.g. Felber et al., 2015; Coates et al., 2017). While other authors used also automatic GPS tracking (e.g. Felber et al 2016 in AEE) the authors manually attributed the animals to a raster. Acknowledging the difficulty to assess a system of wild animals, the method used can be seen as useful first step to quantify bison emissions. A main methodological issue is that the flux uncertainty is underestimated. Knowing that the different footprint models give very different results on which your approach relies upon – to better depict the uncertainty, it would be useful to analyze sensitivity of the CH₄ flux per animal to different footprint models in order to include this uncertainty in the presented SE. The study lacks conclusiveness regarding the bison emission estimate: If the results were robust - What was the reason for the low CH₄ emissions from bisons compared to average cattle emissions?

Thank you for the insightful comments, addressing them improved the manuscript. We added the Kljun et al. footprint model to further characterize uncertainty as suggested. A side-by-side (or similar) comparison between cattle and bison systems would be necessary to understand the mechanisms causing any discrepancy, and we hope that the present manuscript helps justify such an extensive undertaking.

Specific comments

L 21 “Emission estimates are subject to spatial uncertainty in bison location measurements and the flux footprint, but from our measurements there is no evidence that bison methane emissions exceed those from cattle. We caution however that our measurements were made during winter and that evening measurements of bison distributions were not possible using our approach.” The sentence does not make sense. “but” indicates a contrast, while no significant differences are exactly a result of high spatio-temporal variability/and considerable measurement uncertainty.

Please rather give the exact numbers \pm SE for both estimates, for so the readers get an idea of what it means that no differences were found.

We removed the passage for clarity because no direct measurements of cattle were made. Finding adjacent or proximal bison and cattle grazing systems to measure has been an ongoing challenge, and one that we hope to address in future research.

L 25 Eddy covariance is a promising technique for measuring ruminant methane emissions in conventional and alternate grazing systems and can be used to compare them going forward. RC: The

sentence is not really saying much that was not known before. Rather state a concluding sentence from what you found.

We feel that the passage as written is accurate because eddy covariance has not been used to measure methane efflux from non-domesticated animals before. Because our study is in part a proof-of-concept that is important to demonstrate feasibility for future research efforts on non-domesticated ungulates, we made the last line of the abstract more directed and now write, 'Our observations point to the need for direct comparisons of methane emissions from conventional and alternate grazing systems using eddy covariance and demonstrate the potential for using eddy covariance to measure methane efflux from non-domesticated animals.'

Introduction

RC: L43: Add one sentence about: What is known about methane emissions from energy-dense/high-quality versus low-energy/low-quality grass for cattle?

We added 'and feed quality (Hammond et al., 2016)', thank you for the suggestion.

L46: "Methane is a highly potent greenhouse gas and has about 3.7 times the global warming potential of carbon dioxide on a per- mole basis (Lashof and Ahuja, 1990).“ RC: I guess you overlooked some major updates since the nineties – please cite the most recent IPCC report (2014). The number(s) there are considerable higher...

We deleted the passage because these comparisons rely on a subjective time window and the readership of Biogeosciences is familiar with the importance of methane as a greenhouse gas.

L49: Between 30 and 40 percent of anthropogenic methane emissions are due to enteric fermentation in livestock

We clarified this passage to state 'current' anthropogenic methane emissions.

L60 "The important role of bison to past methane fluxes suggests that current their role in the global methane budget must be understood as their populations increase." The sentence does not make sense, improve spelling/grammar.

Thank you for the suggestion the passage was re-worded for clarity.

L 63: 30 L per kg dry food intake – how does this compare to measurements from cattle? The number is not very meaningful without comparison as a reference

These are simply the results presented by Galbraith et al. who did not measure cattle in their study. In the revised manuscript we cite cattle values from Hammond et al., 2016 who used a similar technique and found nearly identical values 16.5 g methane / kg dry matter intake (= 29.8 L methane / kg dry

matter intake) when feeding dairy cattle a high maize silage; thank you for suggesting that we dig into this topic further.

Methods

If you provide hay, how are the feeding values typical for what they would eat otherwise? I would guess the hay represents rather an average, not particularly species selected to be nutrient-rich.

The landowners provide supplemental hay from a nearby field. Upon further request, we were sent extensive tables of the hay nutrient content and feed and we will summarize these as supplemental material noting that bison were also free to graze within the pasture. In the revision we will provide a version of the following nutrition information and feeding tables. We assume that the forage is of similar quality to whatever pasture grasses the bison are eating, but we were unable to confirm this independently and the bison fed rather vigorously on the supplemental hay.

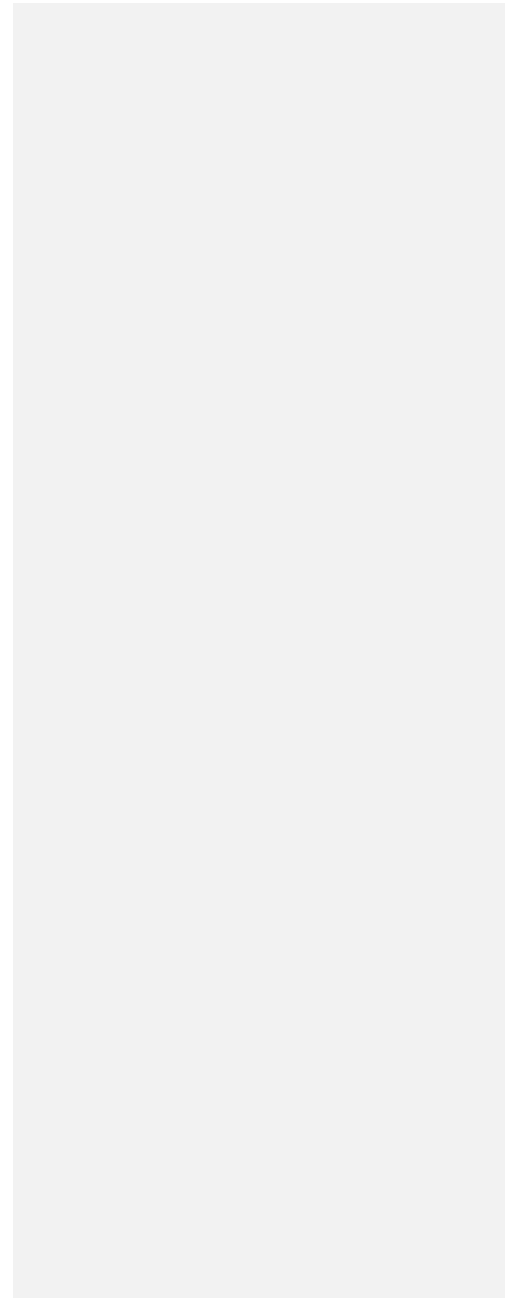
Table 1: Composition of the first cut and second cut hay provided as a supplement to the study bison herd.

Variable (% unless otherwise noted)	First cut	Second cut
Crude Protein	9.7	17.2
Acid detergent fiber	47.9	38.3
Total digestible nutrients	48.9	59.7
Calcium	0.8	1.51
Phosphorus	0.2	0.21
Magnesium	0.21	0.32
Potassium	1.92	2.06
Sulfur	0.15	0.32
Sodium	<0.011	0.028
Zinc (mg/kg)	14	15
Iron (mg/kg)	66	61
Manganese (mg/kg)	60	56
Copper (mg/kg)	7	9

Table 2: The schedule of bail delivery of first cut and second cut hay to the bison pasture.

	First cut (number of bails)	Second cut (number of bails)
1-Nov	2	2
3-Nov	2	2

5-Nov	1	1
6-Nov	2	2
8-Nov	2	1
10-Nov	2	1
12-Nov	1	1
13-Nov	1	1
14-Nov	1	1
15-Nov		2
16-Nov	1	1
17-Nov	2	2
20-Nov		2
22-Nov	1	2
25-Nov		2
27-Nov	2	2
29-Nov		2
1-Dec		2
3-Dec		
5-Dec	2	2
8-Dec	2	2
12-Dec		2
15-Dec	2	2
19-Dec	2	2
21-Dec	2	2
26-Dec	2	2
28-Dec	2	2
31-Dec	2	2
2-Jan	2	2
5-Jan	2	2
8-Jan	2	2
11-Jan	2	2
15-Jan	2	2
18-Jan	2	2
22-Jan	2	2
26-Jan		2
27-Jan	2	



29-Jan	1	1
31-Jan	1	1
3-Feb	2	2
6-Feb	2	2
10-Feb	2	2
14-Feb	2	2
19-Feb	2	2
22-Feb	2	2
26-Feb	2	2

The methodology for deriving bison location is not clearly described. The perspective of the cameras gives a highly skewed picture. From the description the bison attribution to a grid-cell is not comprehensible. Please describe precisely what you did.

This was a labor-intensive process. We interpreted each five-minute period from multiple cameras and used visual cues in the field (like trees in the background) to note the locations of the animals. Fortunately they were usually congregated in a group which made them relatively easy to place, but wanted to be extremely conservative with our location estimates and their impact on per-animal fluxes, hence the sensitivity analyses.

How can you justify a shift by a grid-cell of 20 m in each direction is sufficient to represent spatial inaccuracies?

Per the response to Referee 1, we were somewhat surprised to find that the precise spatial representation did not make a large difference in per-animal flux estimates. Roughly associating bison to general areas around the tower (following the figure below for one particular half-hour) decreased the per-animal flux estimate by only about 25%. We could be even more conservative with our uncertainty analyses but feel that the Tikhonov Regularization analysis accounts for spatial uncertainties and also provides realistic bounds on per-animal flux values that could be generated. We decided to shift the maps of bison location as an additional check on the sensitivity of the flux values to bison location to provide an even more conservative estimation of uncertainties. We feel that the resulting flux values honestly represent the inherent uncertainties in our analysis.

Please explain to the reader the two-dimensional Tikhonov Regularization (& Lagrange multiplier) in a methods paragraph.

We describe Tikhonov Regularization in more detail in the revised manuscript by expanding section 2.6.

The methods section on the flux calculations could be more specific, i.e. state the respective thresholds and parameters used.

We feel that we were reasonably clear about the flux calculations having indicated spike thresholds but we agree that we could have been more clear about necessary filtering post-processing. We revisited the logical thresholds that we applied to the original dataset after applying the Kljun et al. (2015) flux footprint model and increased the upper limit to 300 micromoles $\text{CH}_4 \text{ m}^{-2} \text{ bison}^{-1}$. Doing so made a small change to average flux values that we feel more confident in because of very intermittent data and large gaps in the histogram at values greater than 300 micromoles $\text{CH}_4 \text{ m}^{-2} \text{ bison}^{-1}$.

The paper would benefit from some numbers indicating: How many datapoints are actually available with e.g. > 20 bisons placed in the area of 60% flux contribution footprint area.

This is an interesting question but we did not feel that it would lead to clarity as each pixel in which bison are located represents a small contribution to the integrated footprint area and the per-bison methane contribution that it represents is embodied in the calculation in equations 1-3.

Results

It necessary to state that winter methane fluxes in the system without bisons are insignificant, as this is a basis for the whole calculation. Still, there are many words spent on this in the results and discussion, I think that this adds not much to the content of the paper.

We agree and took care to minimize the discussion of methane efflux in the absence of bison, but also felt that it was important to describe given potential methane sources in a field that is frequented by wild ungulates (who can jump the fence) and the nearby river (that is not in the dominant wind direction). We still wanted to be very diligent in noting that the field otherwise is near-neutral with respect to methane efflux. We are not sure why that the cautious approach that we take throughout the manuscript is deemed superfluous.

Fig. 7: include the daily variability of fluxes

Previous versions of the text included error bars that made the trends difficult to distinguish and we presented the median rather than the mean to emphasize the bulk of the trends. We worked to create a version that includes error bars and that is hopefully easy to visually interpret and also included x-axis ticks as recommended by Referee #1.

L211 negative not positive

Thank you for noting this error.

In the highly skewed distribution (Fig 11), it is getting obvious that the SE does not represent well the uncertainties. Consider reporting quantiles of the distribution which then reflect the higher uncertainties towards higher CH₄ flux values.

We feel that showing the full probability distribution is the most accurate way of demonstrating the range of values. One might argue that a box and whisker or violin plot may be more appropriate for Figure 7, and we would be inclined to agree, but such a plot would be too busy for the human eye to easily render. We also did not want to burden every value placed with maxima, minima, ranges, and the like and we further point out that we were careful to ensure that negative flux values remained in our per-bison flux estimates, rather than thresholding the values at zero, which can bias the full uncertainty distribution of the observations.

It would be useful and interesting to repeat the measurements with the fodder source placed in the major footprint area.

Bison and the flux footprint both tended to reside in the south, southwest, and west ends of the pasture. This is a major reason why we chose the particular experimental design. It would be an interesting additional experiment to place feed within the footprint, but this might amount to flux chasing. Bison are powerful and unpredictable animals and entering their enclosure would be very risky (and certainly not allowed by the University). Fodder was delivered by the employees of the landowner over the fence from a safe distance.

From Fig 3 and Fig 6 it becomes clear how little overlap there is between bison presence in the footprint. How would the flux estimates look like if you just choose the occasions when the joint presence of many bison overlaps with the core (i.e. 50% flux contribution) footprint area for a certain time? Such an analysis could enhance the understanding of how robust your estimate is.

Figure 3 represents a half-hour period and Figure 6 the aggregated flux footprint, which lies predominantly to the southwest. Bison tended to aggregate to the west such that there was considerable overlap between bison and footprint distributions. We do not know how this conclusion was arrived at given that the footprint and bison favored the areas west, southwest, and south of the tower. We recreated the figures to demonstrate the overlap between bison and footprint given that we carefully designed the experiment to ensure reasonable overlap between the footprint and bison distributions.

Discussion

Give an approximate estimate of the bulk uncertainties inherent to the flux calculations in the discussion section.

We feel that we did this in the opening paragraph of the Discussion.

It remains unclear if the low CH₄ fluxes for bison fluxes is a result of methodology (spatial distribution, flux footprint uncertainty, non-stationary conditions) and possibly (but probably of much less importance) also other confounding factors (fodder composition).

We agree but could not test bison methane efflux with respect to diet directly without a calorimeter (and permission from the landowner and University to make such a measurement, neither of which would be likely to be granted and further the animal may have to be sedated and/or at a lower metabolic state to be in a box, resulting in measurement bias). We suspect that a major reason for low methane fluxes is due to energy conservation during winter and hope to confirm this by securing grant funding for a larger study to do so. The seasonal cycle of cattle methane efflux is apparent in Prajapati and Santos (2019) and other references who often assume that the seasonal variability may be due to changes in background sources in their feedlot system. We are curious to know how seasonal metabolic effort impacts CH₄ efflux and expanded the discussion of this topic in the revised manuscript.

In the discussion, it is necessary to more specifically elaborate on why bison CH₄ emissions should be that low, what can be reasons/mechanisms behind it?

We were hesitant to speculate on the reasons for the relatively low per-animal methane efflux but do note that they are rather similar to Prajapati and Santos (2019) and other values from cattle in winter. We note this more explicitly in the revised manuscript. As noted in the above comment we suspect that wintertime energy conservation is a dominant reason and we are interested in exploring seasonal variability in methane efflux further.

The methodological issues seem to dominate the outcome of the paper and I lack of confidence in the estimated uncertainty.

We disagree. We treated methodological challenges with an abundance of caution and state this extensively in the text. We included two sensitivity analyses with respect to the footprint analysis that is now extended to include an independent footprint model. We feel that this exceeds the uncertainty analyses of most eddy covariance-based studies.

Methane efflux from an American bison herd

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Abstract. American bison (*Bison bison* L.) have recovered from the brink of extinction over the past century. Bison reintroduction creates multiple environmental benefits, but impacts on greenhouse gas emissions are poorly understood. Bison are thought to have produced some 2 Tg year⁻¹ of the estimated 9-15 Tg year⁻¹ of pre-industrial enteric methane emissions, but few contemporary measurements have been made due to their mobile grazing habits and safety issues associated with direct measurements. Here, we measure methane and carbon dioxide fluxes from a bison herd on an enclosed pasture during daytime periods in winter using eddy covariance. Methane emissions from the study area were negligible in the absence of bison (mean ± standard deviation = $-0.0009 \pm 0.008 \mu\text{mol m}^{-2} \text{s}^{-1}$) and were significantly greater than zero, $0.048 \pm 0.082 \mu\text{mol m}^{-2} \text{s}^{-1}$ with a positively skewed distribution, when bison were present. We coupled bison location estimates from automated camera images with two independent flux footprint models to calculate methane efflux on a per-animal basis, which varied from $55 \mu\text{mol s}^{-1} \text{bison}^{-1}$ to $62 \mu\text{mol s}^{-1} \text{bison}^{-1}$. Per-animal methane efflux estimates were also sensitive to uncertainties in bison location, and sensitivity analyses suggest that a conservative uncertainty estimate is on the order of 22%. Combined with conservative uncertainty estimates of the eddy covariance measurements themselves, we arrive at methane flux estimates of $76 \pm 21 \text{ g CH}_4 \text{ bison}^{-1} \text{ day}^{-1}$ when using the Hsieh et al. (2000) model and $86 \pm 24 \text{ g CH}_4 \text{ bison}^{-1} \text{ day}^{-1}$ when using the Kljun et al. (2015) model, similar to eddy covariance measurements of methane efflux from a cattle feedlot during winter. Annual measurements are ultimately necessary to determine the full greenhouse gas burden of bison grazing systems. Our observations point to the need for direct comparisons of methane emissions from conventional and alternate grazing systems using eddy covariance and demonstrate the potential for using eddy covariance to measure methane efflux from non-domesticated animals.

1 Introduction

The American bison (*Bison bison* L.) was hunted to near extinction during European expansion across North America (Flores 1991, Isenberg 2000, Smits 1995). Fewer than 100 reproductive individuals existed on private ranches in the United States

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during the late 19th Century from an original population of 30 – 60 million (Hedrick, 2009). The current bison population of about 500,000 is due to the collective efforts of sovereign Indian tribes, government agencies, and private landowners (Gates et al., 2010; Sanderson et al., 2008; Zontek, 2007). [all of whom have spurred a growing interest in bison reintroduction. The bison population is](#) likely to further increase, increasing the incentive for researchers and land managers to understand the environmental impacts of their expansion.

The ecological role of bison has become better understood as populations have recovered (Allred et al., 2001; Hanson 1994; Knapp et al., 1999). Bison feed preferentially on grasses (Plumb and Dodd, 1993; Steuter and Hidinger, 1999) and enhance forb diversity as a result (Collins, 1998; Hartnett et al., 1996, Towne et al., 2005). They tend to graze in preferred meadows during winter and search broadly for the most energy-dense forages in summer (Fortin et al., 2003), often in areas which have recently burned (Allred et al., 1991; Coppedge and Shaw, 1998; Vinton et al., 1993). Bison also [need](#) not migrate to follow the 'green wave' of fresh vegetation during spring green-up like other ungulates; rather, their vigorous grazing tends to stimulate plant growth and create fresh, nutrient-rich foliage (Geremia et al., 2019). Combined, these observations suggest that bison select for forage quality rather than quantity which likely impacts their efflux of methane – which all ruminants emit – because ruminant methane emission is related to the cellulose and hemicellulose intake of their diet (Moe and Tyrrell, 1979) [and feed quality \(Hammond et al., 2016\)](#). It remains unclear how much methane results from the cellulose-rich grass-dominated diet of bison given their preference for fresh foliage and if management for bison may increase or diminish the greenhouse gas burden of ruminant-based agriculture.

Atmospheric methane concentrations have been rising at an accelerated rate since 2016 for reasons that remain unclear (Nisbet et al., 2019) and there is an urgent need to improve our understanding of its surface-atmosphere flux. Between 30 and 40 percent of [current](#) anthropogenic methane emissions are due to enteric fermentation in livestock (Kirschke et al., 2013) and the greenhouse gas burden of cattle alone is some 5 Pg of carbon dioxide equivalent per year (Gerber et al., 2013; FAO, 2017). Recent studies have revised methane emission estimates from livestock upward by over 10% (Beauchemin et al., 2008; Thornton and Herrero, 2010; Wolf et al., 2017), further emphasizing their critical role in global greenhouse gas budgets [\(Reisinger and Clark, 2017\)](#). Reducing unnecessary greenhouse gas emissions is a global imperative for Earth system management and reducing enteric methane sources is seen as a promising approach to do so (Boadi et al., 2002; DeRamus et al., 2003; Herrero, et al., 2016; Hristov et al., 2013; Johnson and Johnson, 1995; Moss et al., 2000).

Bison in North America are thought to have been responsible for some 2.2 Tg year⁻¹ (Kelliher and Clark, 2010; Smith et al., 2016) of the 9-15 Tg year⁻¹ of pre-industrial enteric methane emissions (Thompson et al., 1993; Chappellaz et al., 1993; Subet, 1994). Enteric CH₄ emissions from wild ruminants in the United States in the pre-settlement period comprised [nearly 90%](#) of current CH₄ emissions from domesticated ruminants assuming an historic bison population size of 50 million (Hristov, 2012). [Further demonstrating the importance of bison to methane fluxes in the past. The current and future contribution of non-domesticated ungulates to methane fluxes are uncertain \(Crutzen et al., 1985\)](#). Previous approaches used inventory approaches or scaling equations that were not derived using methane efflux measurements from bison; the only direct bison methane flux observations that we are aware of measured 30 L per kg dry food intake [\(17 g methane per kg dry food intake\)](#) in one-year-old

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05 panned female bison fed alfalfa pellets (Galbraith et al., 1998), more than elk (*Cervus elaphus*) and white-tailed deer (*Odocoileus virginianus*) on a dry matter intake basis, and similar to dairy cattle fed high maize silage (Hammond et al., 2016). Cattle methane emissions tend to be greater when fed alfalfa than grass (Chaves et al., 2006) such that existing published values may not represent an accurate estimate of the methane efflux from bison in a natural field setting, which has not been measured to date.

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10 Here, we measure methane flux from a bison herd on winter pasture using the eddy covariance technique (Dengel et al., 2011; Felber et al., 2015; Prajapati and Santos, 2018; Sun et al., 2015). We use flux footprint analyses combined with bison locations determined using automated cameras to estimate methane flux on a per-animal basis and discuss observations in the context of eddy covariance methane flux measurements from other ruminants.

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2 Methods

2.1 Study site

15 The study site is a 5.5-hectare pasture on the Flying D Ranch near Gallatin Gateway, Montana, USA (45.557, -111.229) on a floodplain immediately west of the Gallatin River (Figure 1). Daily high temperatures average 1.6 °C and daily low temperatures average -11.5 °C at Bozeman, Yellowstone International Airport (BZN), located 24 km north-northeast of the site, during the November – February measurement period. BZN records an average of 18.2 mm of precipitation per month during November – February, almost entirely as snowfall. A herd of 39 bison entered the pasture on November 17, 2017 and left on February 3, 2018. The mean (standard error) bison weight measured by the landowners on November 16, 2017 before bison entered the pasture was 329 ± 28 kg and the bison varied in age from 0.5 to 7.5 years old (Table S1). Bison consumed a mixture of perennial grasses grown *in situ* that was supplemented by perennial grass hay grown in nearby fields (Table S2) delivered every three days on average (Table S3).

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2.2 Instrumentation

125 A 3 m tower was installed near the center of the study pasture during November 2017 (Figure 1) and surrounded by electric fencing to avoid bison damage. Four game cameras (TimelapseCam, Wingscapes, EBSCO Industries, Inc., Birmingham, AL, USA) were mounted to the tower and pointed in cardinal directions. Two additional game cameras were mounted near the pasture edge facing the tower. Cameras captured images every five minutes and an example of an individual image from the south-facing camera located on the northern edge of the study pasture is shown in Figure 2. Bison locations at the half-hourly time interval of the eddy covariance measurements were estimated by manually attributing bison locations to squares in a 20 m grid overlaid on the pasture area (Figure 1). The 20 m grid size represents the grid that we felt that we were able to attribute bison locations given features of the field that could be identified by camera. The bison location approach introduces

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150 [uncertainty, and we](#) test the sensitivity of [per-animal methane efflux estimates](#) to bison location estimates as described in the *Spatial Uncertainty* section below.

155 Incident and outgoing shortwave and longwave radiation and thereby the net radiation were measured using a NR01 net radiometer (Hukseflux, Delft, The Netherlands) mounted 1.5 meters above ground level. A SR50 sonic distance sensor (Campbell Scientific Inc., Logan, UT, USA) was installed at 1.3 m to gauge snow depth, and air temperature and relative humidity were measured at 2.25 meters using a HMP45C probe (Vaisala, [Vantaa](#), Finland). Average [0–30 cm](#) soil moisture and temperature were collected using CS650 probes (Campbell Scientific). Meteorological variables were measured once per minute, and half-hourly averages were stored using a CR3000 datalogger (Campbell Scientific).

160 Three-dimensional wind velocity was measured using a CSAT-3 sonic anemometer (Campbell Scientific) at 2.0 m above the ground surface. Carbon dioxide mixing ratios were measured at 10 Hz using a LI-7200 closed-path infrared gas analyzer (LI-COR Biosciences, Inc.) with inlet placed at the same height as the center of the sonic anemometer. Methane mixing ratios were measured at 10 Hz using a LI-7700 open-path infrared gas analyzer (LI-COR Biosciences, Inc., Lincoln, NE, USA) with the center of the instrument likewise located at 2.0 m [and a 22 cm horizontal offset from the sonic anemometer](#); [open- and closed-path infrared gas analyzers](#) for eddy covariance have [similar performance](#) in field settings (Detto et al., 2011; Deventer et al., 2019). We use the atmospheric convention in which flux from biosphere to atmosphere is positive. Measurements were made during [winter](#) daytime hours from 0700 to 1700 local time to avoid depleting the battery bank and to ensure sufficient light to estimate bison location using game cameras. Flux measurements began on November 14, 2017 and ended on February 14, 2018.

170 [Bison](#) are dangerous and will charge humans. [Their](#) presence complicated data retrieval and game camera upkeep; some high-frequency flux measurements were overwritten and cameras shut down during exceptionally cold periods, resulting in missing measurements. Simultaneous flux and photographic data were obtained for the January 7, 2018 to February 13, 2018 period excluding January 10, 2018 when instruments were obstructed by snowfall. Flux data without accompanying game camera footage were obtained for the periods from November 14 through 29, 2017 and December 31, 2017, through January 6, 2018.

2.3 Flux [calculations](#)

175 Methane and carbon dioxide fluxes were calculated using EddyPro (LI-COR Biosciences, Lincoln, NE, USA). Standard double rotation, block averaging, and covariance maximization with default processing options were applied. Spike removal was performed as described by Vickers and Mahrt (1997) and spikes were defined as more than 3.5 standard deviations from the mean mixing ratio for carbon dioxide and more than 8 standard deviations from the mean mixing ratio for methane given the expectation of intermittent methane spikes from the bison herd. The default drop-out, absolute limit, and discontinuity tests were applied using the default settings following recommendations by Dumortier et al. (2019), and the Moncrieff et al. (1997) and Moncrieff et al. (2004) low and high-pass filters were applied. The Webb-Pearman-Leuning correction (Webb et al., 1980) was applied to calculate methane efflux using the open-path LI-7700 sensor. [Estimates of storage flux in the 2 m airspace](#)

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190 below the infrared gas analyzers were assumed to be minor and excluded from the flux calculation. Flux measurements for
which the quality control flag was greater than 1 following Mauder and Foken (2004) (see also Foken et al., 2004) were
discarded, and the net effect of all corrections when bison were present was a methane flux reduction of 14%. Measurements
195 that exceeded an absolute value of $1 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the case of methane flux and $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the case of carbon dioxide
flux were discarded following an analysis of the probability distribution of observations. We tested the sensitivity of flux
measurements to the friction velocity (u^*) to see if measurements made under conditions of insufficient turbulence should be
excluded from the analysis despite the daytime-only flux measurement approach.

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2.4 Flux footprint modelling

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The eddy covariance flux footprint was calculated using the approach of Hsieh et al. (2000) extended to two dimensions following Detto and Katul (2006). Such analytical footprint models have been found to give minimally biased estimates of
200 point-source fluxes in field settings (Dumortier et al., 2019). We performed the footprint analysis on a grid of 1 m pixels and aggregated values to the 20×20 m grid to which the bison locations were estimated (Figure 1); Figure 3 demonstrates an example of a flux footprint for a single half-hourly period.

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To further characterize the uncertainty in our per-animal methane flux estimates, described next, we also applied the flux footprint parameterization method of Kljun et al. (2015) aggregated to the same 20×20 m grid. The Kljun et al. (2015) model performs well in point-source experiments (Heidbach et al., 2017) and is widely used by the flux community.

The momentum roughness height (z_{0m}) is required by both footprint models. Instead of assuming a constant z_{0m} over snow of 0.001 m (Andreas et al., 2004), we followed the approach of Baum et al. (2008) who calculated a unique z_{0m} for each half-hour eddy covariance measurement for a cattle feedlot system by rearranging the wind profile equation:

$$z_{0m} = \frac{z - d}{\exp(ku/u_* + \psi_m)} \quad (1)$$

210 Where z is measurement height, u is wind speed, k is the von Karman constant, and ψ_m is the correction factor for atmospheric stability, here following Brutsaert (1982). The zero-plane displacement (d) for a field with obstacles is calculated following Verhoef et al. (1997):

$$d = z - \frac{z(1 - \exp(-\sqrt{4z\alpha}))}{\sqrt{4z\alpha}} \quad (2)$$

where α is the frontal area index of the obstacles (Raupach, 1994), here bison:

$$a = \frac{nbh}{S} \quad (3)$$

215 The calculation of a uses the number of animals ($n = 39$), the size of the pasture (S , m^2), and the average breadth (b , m) and height (h , m) of the animals. We used established relationships for beef cattle as a function of weight (ASABE, 2006) given the lack of similar equations for bison. h was adjusted upward by 50% such that the height of adult males better-matched average values of fully-grown bison on the order of 1.8 m. The methane source location was assumed to be near the ground per the typical posture of bison assuming that most methane efflux in ruminants is from eructation.

225 **2.5 Per-bison methane flux estimation**

Given that mean methane emissions were not significantly different from zero in the absence of bison – as detailed in *Results* – we assume that observed methane emissions are due to bison in the flux footprint. The relative contribution of bison to each half-hourly eddy covariance measurement was calculated by expanding the approach of Dumortier et al. (2019) (see also Prajapati and Santos (2019)) for multiple point sources. From the definition of the footprint function, the measured density of a scalar X , F_X , for our study area of 8×12 grid cells (Figure 1) is:

$$F_X = \sum_{i=1}^8 \sum_{j=1}^{12} F_{ij} \phi_{ij} \Delta x_{ij} \Delta y_{ij}$$

where ϕ_{ij} is the value of the footprint function in grid cell ij (here per 400 m^2) and x and y are the dimensions of the 20 m grid cells. Dumortier et al. (2019) considered a known point source from a single cell, f_x , such that:

$$f_x = \frac{F_X}{\phi_{ij,source}}$$

where $\phi_{ij,source}$ is the value of the footprint function at the source location. We have $n = 39$ sources (i.e. bison) that are free to wander to any grid cell ij . We also have no basis for identifying individual bison given the resolution of the cameras, noting that this is possible using higher-resolution cameras (Merkle and Fortin, 2013) or GPS instruments. We also have no basis for determining if the methane sources of individual bison are different using our approach, so we must assume that methane efflux from each bison is equal. Under these assumptions we can write:

$$\langle f_x \rangle = \frac{F_X}{\sum_{i=1}^8 \sum_{j=1}^{12} n_{ij} \phi_{ij} \Delta x_{ij} \Delta y_{ij}}$$

Where n_{ij} is the number of bison in grid cell ij (i.e. per 400 m^2) and $\langle f_x \rangle$ is the average flux per bison. We only adopt this approach for calculating average methane efflux per bison as measured carbon dioxide fluxes in the absence of bison were greater than zero. Methane efflux values less than $-200 \mu\text{mol bison}^{-1} \text{ s}^{-1}$ and greater than $300 \mu\text{mol bison}^{-1} \text{ s}^{-1}$ were treated as outliers and excluded based on an analysis of the probability distribution of observations.

240 **2.6 Spatial uncertainty**

The location of bison in the pasture was approximated visually by identifying the position of bison in relation to static cues in the study area using five-minute photographs. Observations were then aggregated to half-hourly flux measurement periods. This approach results in spatial uncertainty in bison location, especially due to movements within half-hourly periods and due to the size of the animals themselves with reference to the grid (Figure 1). Both will result in a greater spatial distribution of bison locations than represented in the maps of bison distributions that were created. To arrive at a conservative estimate of uncertainty in per-bison methane flux estimates, we explored the sensitivity of flux estimates to maps of bison location that were more distributed in space. To do so we used two-dimensional Tikhonov Regularization (Tikhonov and Arsenin, 1977), a

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classic mathematical technique to solve ill-posed problems, here the challenge of estimating the best spatial distribution of bison with intermittent observations.

To briefly describe the motivation for using Tikhonov Regularization for our case, consider the extreme distributions of potential bison locations: all are located in a single grid cell (a Dirac delta function) or all are perfectly aggregated across the field (an uninformed prior). The true distribution likely exists between these cases, especially given intermittent bison movements. The estimates of their location using cameras provides an initial guess of the true location. We assume that the true number of each bison in each pixel is likely to be similar to those measured in adjacent pixels because the bison movements were usually minor and because of the uncertainty that exists when attempting to associate bison to a particular pixel. Two-dimensional Tikhonov Regularization can provide an estimate of the true distribution of elements (here bison) given the constraints that the distribution is bounded and that adjacent pixels are likely similar to a given pixel (Stoy and Quaiife, 2015). We use a form of Tikhonov Regularization to create spatial disaggregation of each bison distribution map (α') following Stoy and Quaiife (2015):

$$\alpha' = \alpha(I + \gamma^2 B^T B)^{-1} \frac{\sigma^2}{\psi(\gamma^2)} - \mu_\alpha + \mu_{\alpha'}. \quad (7)$$

Here, α is the measured distribution map with mean μ_α (the number of bison per pixel) and variance σ , I is the identity matrix, B represents the constraint that neighboring elements should be similar by requiring a first difference of zero in the cardinal directions of the map, γ is the Lagrange Multiplier, and $\psi(\gamma^2)$ is a normalization term equal to the variance of $\alpha(I + \gamma^2 B^T B)^{-1}$. Large values γ constrain each pixel to be near the overall mean such that the bison distribution map is smoother across space.

We applied the Tikhonov Regularization approach to each bison distribution map using Lagrange multipliers that ranged from 0.1 to 4 as demonstrated for a single half-hour period in Figure 4; note that the simulation with a Lagrange multiplier of 4 results in a simulation where bison are widely distributed across segments of the field and amounts to a highly conservative estimate of their location. Our results are subject to simultaneous uncertainties in footprint and bison location in addition to the eddy covariance methane flux measurements themselves, which range from 6 – 41% for half-hourly fluxes and 7 – 17% for long-term sums (Deventer et al., 2019). We use 17% as a representative uncertainty of eddy covariance sums as we are primarily concerned with providing a conservative assessment of uncertainty using our approach. We suggest strategies for reducing uncertainty in the Discussion section.

3. Results

3.1 Meteorology

Air temperature averaged -2.8 °C and soil temperature averaged -0.3 °C during the measurement period (Figure 5A). Incident shortwave radiation ranged between 100 and 400 W m^{-2} during peak daylight hours (1000-1400 hours local time) across the study period, and clear conditions were common except for four weeks beginning in mid-December (Figure 5B). Snow depth within the tower enclosure increased from 0.15 m to nearly 0.4 m in late 2017 and decreased to 0.1 m beginning in late January 2018 (Figure 5C) noting that snow outside of the electrified tower enclosure was often trampled (see Figure 2). The mean

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(median) wind direction was 221° (208°) during periods when visible imagery of bison locations was available and eddy covariance measurements passed quality control checks (Figure 6).

315 3.2 Gas flux

Half-hourly methane fluxes averaged $0.048 \pm 0.081 \mu\text{mol m}^{-2} \text{s}^{-1}$ (mean \pm standard deviation) and carbon dioxide fluxes averaged $1.6 \pm 1.4 \mu\text{mol m}^{-2} \text{s}^{-1}$ when bison were present (Figure 7), noting again that measurements were made only during daytime periods. Methane flux in the absence of bison averaged $-0.0009 \pm 0.008 \mu\text{mol m}^{-2} \text{s}^{-1}$ and carbon dioxide flux averaged $0.64 \pm 1.0 \mu\text{mol m}^{-2} \text{s}^{-1}$, significantly lower than when bison were present ($P < 0.001$ for both CH_4 and CO_2). CO_2 flux was significantly related to methane flux and explained 52% of its variance when bison were present but only 7% when they were absent (Figure 8). CO_2 flux was significantly and positively related to air and soil temperature across the entire measurement record ($P < 0.001$ in both cases), but methane flux was not. There were no significant temporal patterns of methane flux during the daytime periods investigated here, and neither incident nor net radiation were related to methane fluxes. When bison were present, methane flux was not significantly different at the $P < 0.05$ significance level during days when feed was delivered ($0.051 \pm 0.083 \mu\text{mol m}^{-2} \text{s}^{-1}$) and days when it was not ($0.035 \pm 0.10 \mu\text{mol m}^{-2} \text{s}^{-1}$) ($P = 0.075$).

Methane flux was significantly and positively related to friction velocity in the absence of bison at u^* values greater than 0.2 m s^{-1} ($P = 0.003$) but not positively related to u^* values less than 0.2 m s^{-1} , indicating that flux measurements were unrelated to friction velocity values commonly associated with insufficient turbulence (Figure 9A). Carbon dioxide flux was not related to u^* in the absence of bison (Figure 9B) but negative values were observed at u^* values greater than 0.45 m s^{-1} . Given these observations, we did not apply a u^* filter to our eddy covariance measurements, which were made only during daytime periods. We discuss potential reasons for the observed increase in methane flux and negative CO_2 flux with high values of u^* in the Discussion section.

330 3.3 Bison location and methane efflux

Timelapse camera footage yielded usable imagery for 444 half-hourly periods of which 245 half-hourly periods had available eddy covariance observations and of which 177 had eddy covariance measurements that passed quality control criteria. Bison tended to aggregate in an area on the west side of the pasture near the location where supplemental hay was often provided (Figure 10A). They intermittently visited the area north of the tower in mornings and afternoons and intermittently made sporadic mass movements to the southernmost edge of the field near its gate during midday periods (Figure 10B-D).

Bison were located within the 90% flux footprint 40% of the time (Figure 11). There was an average of eight (seven bison within the 90% flux footprint of the Hsieh et al. (2000) (Kljun et al. (2015)) models which increased to both footprint models which increased to 21 (20), respectively, when excluding observations with no bison (Figure 11). Per-bison methane emission estimates when using the Hsieh et al. (2000) footprint model had a mean (\pm standard error) of $55 \pm 0.96 \mu\text{mol bison}^{-1} \text{s}^{-1}$ and a median of $29 \mu\text{mol bison}^{-1} \text{s}^{-1}$ as a result of the positively skewed measurement distribution (Figure 12A). These estimates

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are 11% lower than per-bison methane emission estimates from the Kljun et al. (2015) footprint model, which returned a mean (\pm standard error) of $62 \pm 0.91 \mu\text{mol bison}^{-1} \text{ s}^{-1}$, which demonstrates that per-animal flux estimates are sensitive to flux footprint methodology. Per-animal flux estimates are also sensitive to the estimates of their location within the field; mean methane flux estimates ranged from $43 - 58 \mu\text{mol bison}^{-1} \text{ s}^{-1}$ when applying the Hsieh et al. (2000) model and $50 - 75 \mu\text{mol bison}^{-1} \text{ s}^{-1}$ when applying the Kljun et al. (2015) model after spatial smoothing using Tikhonov Regularization. These estimates are up to 22% different than the mean methane flux estimates that were generated by taking the maps at face value. If we adopt 22% as a conservative uncertainty estimate due to spatial uncertainty and 17% as a conservative uncertainty estimate of long-term methane flux sums (Deventer et al., 2019) for a combined uncertainty of 28%, we arrive at a daily per-bison methane flux estimate of $76 \pm 21 \text{ g CH}_4 \text{ bison}^{-1} \text{ day}^{-1}$ when using the Hsieh et al. (2000) footprint model and $86 \pm 24 \text{ g CH}_4 \text{ bison}^{-1} \text{ day}^{-1}$ when using the Kljun et al. (2015) footprint model.

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4 Discussion

The eddy covariance flux footprint analysis coupled to bison location estimates from automated camera images resulted in a mean (median) methane flux of 55 (29) $\mu\text{mol bison}^{-1} \text{ s}^{-1}$ when applying the Hsieh et al. (2000) footprint model and 62 (43) $\mu\text{mol bison}^{-1} \text{ s}^{-1}$ when applying the Kljun et al. (2015) footprint model. Measurements were made during daytime periods in winter and are sensitive to estimates of bison location (Figure 12). If we naively assume that methane flux from bison varies negligibly across the full diurnal and seasonal range, a notion that needs to be substantiated, our measurements with conservative uncertainty estimates correspond to 26 ± 8 (31 ± 9) kilograms of methane per bison per year when applying the Hsieh et al. (2000) (Kljun et al. (2015)) model, noting that methane emissions from cattle have been observed to be on the order of 10-17% higher in summer than winter (Todd et al., 2014; Prajapati and Santos, 2018; Prajapati and Santos, 2019) but lower in evenings if animals eat less during these times (Gao et al., 2011). The mean weight of the study bison herd was 329 kg, similar to the 300 kg buffalo that is assumed to emit 55 kg year^{-1} in the 2006 IPCC report (IPCC 2006) noting that dairying buffalo cows are estimated to have higher methane emissions than other buffalo (C6ndor et al. 2008). The study herd here comprised numerous pregnant females (Table S1) that have higher metabolic requirements. Previous estimates of methane emissions from range cattle are on the order of 60 kg per year per animal (Hogan, 1993), about twice as large as the mean per-bison methane flux calculated here. Values were instead similar to the lower range measurements from young heifers feeding on ryegrass of $88 \text{ g CH}_4 \text{ animal}^{-1} \text{ day}^{-1}$ (Hammond et al., 2016) and wintertime measurements of beef cattle in a feedlot on the order of $75 \text{ g CH}_4 \text{ animal}^{-1} \text{ day}^{-1}$ (Prajapati and Santos, 2019). In other words, while there is no evidence from our measurements that bison have more or less methane efflux than typical values reported for cattle, it is critical to make full year-round methane flux measurements with uncertainty to understand the seasonal course of bison methane efflux to establish defensible annual sums. Below, we discuss potential reasons for the relatively low bison methane emissions observed here as well as a strategy for reducing uncertainty in eddy covariance measurements of methane efflux from grazing non-domesticated ruminants.

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4.1 Bison methane and carbon dioxide efflux in response to environmental variables

Methane flux was not related to air or soil temperature but was related to u^* – especially at relatively high values of u^* – in the absence of bison (Figure 9). These observations are consistent with a potential pressure pumping mechanism for trace gases through snow at higher wind speeds (Bowling and Massman, 2011) although it is unclear why this relationship exists for methane flux and not carbon dioxide flux as is frequently found in snow-covered conditions (Rains et al., 2016). Carbon dioxide flux at high values of u^* was [negative](#) indicating net CO₂ uptake by the biosphere, which is unlikely in our study site during winter, suggesting that values with excessively high u^* may need to be filtered, but with only five observations of CO₂ flux less than zero it is unclear how to apply such a filter [in our case](#).

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Insufficient evidence exists in our data record to attribute observed methane efflux to the onset of freezing conditions in soil (Mastepanov et al., 2008). We note that extensive snow trampling (e.g., Figure 2) likely resulted in a situation where snow depth (Figure [5C](#)) and its insulating effect on soil temperature (Figure 5A) varied across the field and therefore differed from [snow and soil](#) measurements taken [within the instrumentation enclosure](#). Regardless, mean methane flux when bison were absent, $-0.0009 \mu\text{mol m}^{-2} \text{s}^{-1}$, was nearly two orders of magnitude less than the mean methane flux when bison were present, $0.041 \mu\text{mol m}^{-2} \text{s}^{-1}$. Whereas we cannot exclude – and in fact expect – positive and negative background methane fluxes from

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non-bison sources in a grassland in winter in the vicinity of a riparian area (Figure 1, Merbold et al., 2013; McLain and Martens, 2006; Mosier et al., 1991), these appear to be minor compared to the CH₄ flux attributable to bison (Figures 7 and 8). Bison are associated with a distinct methane flux signature as shown by the immediate decline of methane fluxes following their removal from the study pasture (Figure 7) and strong relationship with carbon dioxide flux (Figure 8) given the common source of respiration and most enteric methane losses from the mouths of ungulates. Methane flux was related to carbon dioxide flux when bison were present or absent (Figure 8), suggesting both soil and ruminant sources (and in the case of methane sinks) of both gases (Baldocchi et al., 2012; Motte et al., 2019).

It is important to note that potential methane fluxes from bison manure may have been dampened by freezing conditions but are an important methane source during warmer conditions in ruminant grazing systems (Dengel et al., 2011). Manure is thought to contribute a nontrivial portion (10-14 Tg CH₄ yr⁻¹) of total [global](#) ruminant methane efflux (77 Tg CH₄ yr⁻¹, Johnson and Ward 1996; Moss et al., 2000) noting that some farm-scale studies arrive at lower percentages (Taylor et al., 2017). Though we did not observe higher methane efflux early in the study period when soil temperature was above freezing nor temperature sensitivity of methane efflux in the presence or absence of bison, it is important to note that field-scale methane efflux may be diminished by the thermal environment of manure in our measurements, [such that methane efflux is lower than would be expected during warmer seasons](#).

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4.2 Bison spatial distribution [and movement](#)

[Ruminant behavior is critical to track to estimate field-scale efflux \(de la Motte et al., 2019\)](#). The spatial distribution of bison in the study pasture varied from morning to midday and afternoon (Figure 10). It is difficult to infer from the available data

whether the study bison are more active during morning and evening hours in the pasture environment like cattle (Gregorini 2012). Supplemental hay was made available to the bison approximately 50 meters west of the tower and increases in the frequency of bison appearance there are likely associated with the animals' preferred feeding times after dawn and before dusk, but observed methane flux did not vary as a function of time of day (e.g. Dengel et al. 2011) and was not significantly different during days when hay was provided and when it was not, noting that the animals were free to also graze on vegetation within the pasture. Regardless, ruminant methane flux measurements are simpler to make when animals congregate (Coates et al., 2017; Tallec et al., 2012) as was often observed here (e.g. Figures 2, 10 & 11). Aggregation behavior in our study bison herd was often upwind of the eddy covariance tower (Figures 6 & 10) and resulted in more overlap between flux footprint and bison location than would have occurred if bison locations were randomly distributed throughout the study area, emphasizing the importance of tower placement in eddy covariance studies of grazing systems.

Spatial uncertainties in bison location interact with uncertainties in flux footprint modelling for methane source attribution (Figure 12). Footprint models of the type used here have been found to accurately estimate point sources of trace gas flux (Heidbach et al., 2017; Dumortier et al., 2019), but it is important to note that footprint modelling techniques play a large role in the spatial attribution of observed fluxes of ruminant trace gas flux (Felber et al., 2015). Prajapati and Santos (2018), for instance, found that an analytical model (Kormann and Meixner 2001) predicted flux footprint areas five to six times larger than did an approximation of a Lagrangian dispersion model (Kljun et al., 2002), such that footprint model uncertainty is a major source of uncertainty for measuring methane flux from multiple point sources as we also found here.

4.3 Future directions for greenhouse gas accounting in ruminant grazing systems

Methane efflux cannot be completely removed from ruminant grazing systems; some 4.6 – 6.2% of gross energy intake is lost as methane in cattle, sheep and goats worldwide (Johnson and Ward 1996) with cattle often falling on the higher end of the observed range (Lassey et al., 1997). But there are other aspects of bison ecology that merit consideration when designing greenhouse gas-cognizant grazing systems. For example, cattle tend to graze close to water more frequently than bison do (Allred et al., 2011) with unclear consequences for riparian vegetation, water quality, and potential methane efflux from cattle wallows. Cattle also tend to graze for longer periods than bison (Plumb and Dodd, 1993) and it is unclear if there is an associated consequence for methane efflux. Future work should consider the large inter-animal variability in methane efflux (Lassey et al., 1997), possibly using advanced techniques for identifying individual animals through photographs (Merkle and Fortin, 2013) or tracking devices (Felber et al., 2015). Animal age and size are also important factors in ruminant methane efflux (Jiao et al., 2014) and individual tracking may improve our estimates of this variability in a field setting.

Adding seasonal foraging behavior, estimating emissions from individual animals, and addressing seasonal and inter-annual variability and trends in forage nutrition are likely to further improve prediction of methane emissions from grazing systems (Moraes et al., 2013). Advanced eddy covariance algorithms for are also likely to improve flux estimates on short time scales

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noting that non-stationary bursts have not been found to create systematic bias in methane budgets measured over longer time periods using eddy covariance (Göckede et al., 2019). Of these, advanced footprint attribution techniques like Environmental Response Functions designed to create improved maps of surface-atmosphere fluxes (Metzger et al., 2013; Xu et al., 2017) may be uniquely applicable to the challenging case presented by grazing systems with mobile point sources and intermittent biogeochemical hotspots created by animal waste. Going forward, increases in atmospheric carbon dioxide concentrations are likely to decrease forage quality (Jégo et al., 2013), resulting in higher leaf carbon to nitrogen ratios and which is expected to increase ruminant methane emissions (Lee et al., 2017), all else being equal. Understanding greenhouse gas fluxes from ruminants is therefore likely to be even more important in the future. An ongoing interest in bison reintroduction and ungulate ecology coupled with established micrometeorological measurement techniques will help us understand the present and future role that bison and alternative grazing systems play in the Earth system.

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Supplemental Information

The land managers provided information that describes bison age, sex, weight, and pregnancy status (Table S1) and the composition (Table S2) and the delivery schedule (Table S3) of hay.

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Code/Data availability

Eddy covariance and micrometeorological data have been submitted to Ameriflux for publication at <https://ameriflux.lbl.gov/sites/siteinfo/US-Tur>.

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Author contributions

PCS designed the study with AC, JD, and WK and wrote the manuscript with all coauthors. AC collected data and analyzed it with PCS and TG. NK assisted with the footprint analysis.

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Competing interests

The authors declare no competing interests.

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Tables

Table S1: The sex, age, and pregnancy status of the study bison with weight measured on November 16, 2017 shortly before they entered the pasture on November 17, 2017. Bison were assumed to be born on June 1 of the birth year by the landowners such that animals born in 2017 were nearly 6 months old when measurements began.

Sex	Age	Weight (kg)	Pregnant
F	7.5	467	Y
F	7.5	419	Y
F	7.5	428	Y
F	7.5	479	Y
F	7.5	510	Y
F	7.5	476	Y
F	7.5	492	Y
F	7.5	454	Y
F	7.5	567	Y
F	7.5	476	Y
F	7.5	497	Y
F	7.5	460	Y
F	7.5	443	Y
F	7.5	435	Y
F	7.5	426	Y
F	7.5	476	Y
F	7.5	411	Y
M	5.5	646	-
M	5.5	701	-
F	3.5	381	Y
F	3.5	410	Y
F	1.5	334	-
F	0.5	110	-
F	0.5	144	-
M	0.5	160	-
F	0.5	166	-
M	0.5	138	-
M	0.5	152	-
M	0.5	147	-
M	0.5	183	-
F	0.5	96	-
M	0.5	208	-
M	0.5	104	-
M	0.5	163	-
F	0.5	127	-
M	0.5	136	-
M	0.5	165	-
M	0.5	126	-
F	0.5	127	-

Deleted: Table 1: The mean and standard deviation of per-bison methane fluxes and corresponding values after shifting the flux footprint matrix 20 meters in the direction indicated by the left column as a sensitivity analysis for bison location estimates.

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Table S2: Composition of the first cut and second cut hay provided as a supplement to the study bison herd.

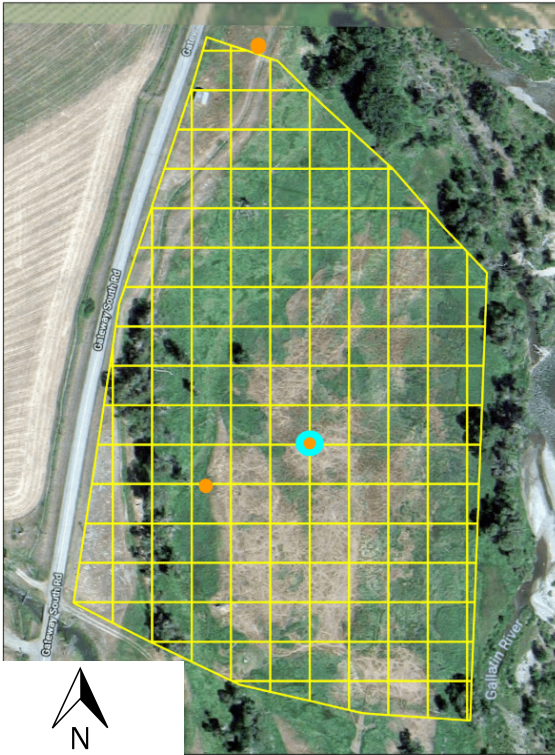
Variable (% unless otherwise noted)	First cut	Second cut
Crude Protein	9.7	17.2
Acid detergent fiber	47.9	38.3
Total digestible nutrients	48.9	59.7
Calcium	0.8	1.51
Phosphorus	0.2	0.21
Magnesium	0.21	0.32
Potassium	1.92	2.06
Sulfur	0.15	0.32
Sodium	<0.011	0.028
Zinc (mg/kg)	14	15
Iron (mg/kg)	66	61
Manganese (mg/kg)	60	56
Copper (mg/kg)	7	9

Table S3: The number of bails of first cut and second cut hay (Table S2) delivered to the bison pasture.

Date	First cut	Second cut
Nov. 17, 2017	<u>2</u>	<u>2</u>
Nov. 20, 2017		<u>2</u>
Nov. 22, 2017	<u>1</u>	<u>2</u>
Nov. 25, 2017		<u>2</u>
Nov. 27, 2017	<u>2</u>	<u>2</u>
Nov. 29, 2017		<u>2</u>
Dec. 1, 2017		<u>2</u>
Dec. 3, 2017		
Dec. 5, 2017	<u>2</u>	<u>2</u>
Dec. 8, 2017	<u>2</u>	<u>2</u>
Dec. 12, 2017		<u>2</u>
Dec. 15, 2017	<u>2</u>	<u>2</u>
Dec. 19, 2017	<u>2</u>	<u>2</u>
Dec. 21, 2017	<u>2</u>	<u>2</u>
Dec. 26, 2017	<u>2</u>	<u>2</u>
Dec. 28, 2017	<u>2</u>	<u>2</u>
Dec. 31, 2017	<u>2</u>	<u>2</u>
Jan. 2, 2018	<u>2</u>	<u>2</u>
Jan. 5, 2018	<u>2</u>	<u>2</u>
Jan. 8, 2018	<u>2</u>	<u>2</u>
Jan. 11, 2018	<u>2</u>	<u>2</u>
Jan. 15, 2018	<u>2</u>	<u>2</u>
Jan. 18, 2018	<u>2</u>	<u>2</u>
Jan. 22, 2018	<u>2</u>	<u>2</u>
Jan. 26, 2018		<u>2</u>
Jan. 27, 2018	<u>2</u>	
Jan. 29, 2018	<u>1</u>	<u>1</u>
Jan. 31, 2018	<u>1</u>	<u>1</u>
Feb. 3, 2018	<u>2</u>	<u>2</u>

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Figures



815 **Figure 1:** The study site near Gallatin Gateway, MT (45.557, -111.229). Bison locations are mapped within the 20-meter grid here superimposed in yellow. The tower location is in cyan and game camera locations are indicated in orange. Background image: Google, Maxar Technologies and the USDA Farm Service Agency ©2018.

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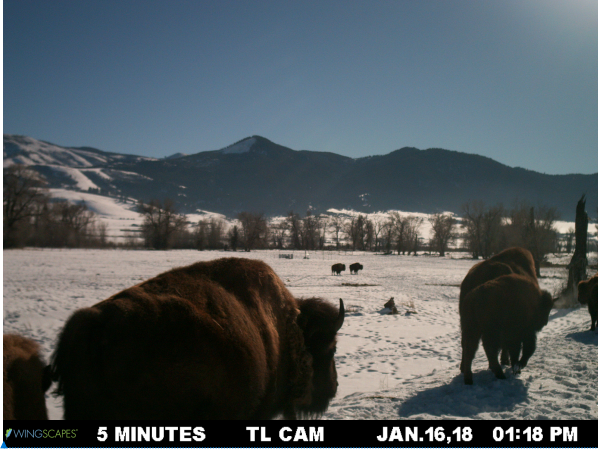
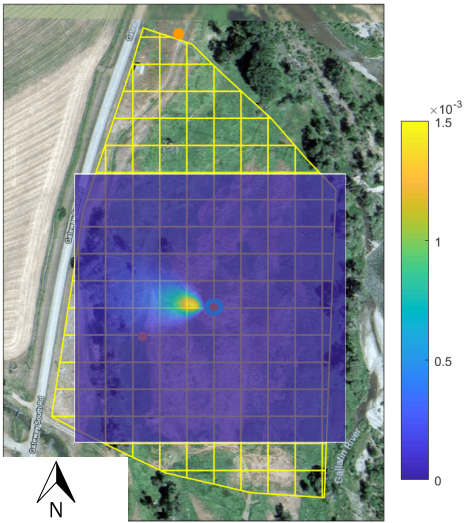


Figure 2: A sample image of bison as viewed from the south-facing time-lapse camera located to the north of the study area (Figure 1). The eddy covariance installation is visible toward the center of the study site.

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820 | Figure 3: An eddy covariance flux footprint calculated following Hsieh et al. (2000) and Detto and Katul (2006) at 1 m resolution for a single 30-minute interval superimposed on the study field (Figure 1). The fraction of the footprint in each grid box is shown in the legend is summed for each 20 m pixel to calculate the contribution of each pixel to the total flux. Background image: Google, Maxar Technologies and the USDA Farm Service Agency ©2018.

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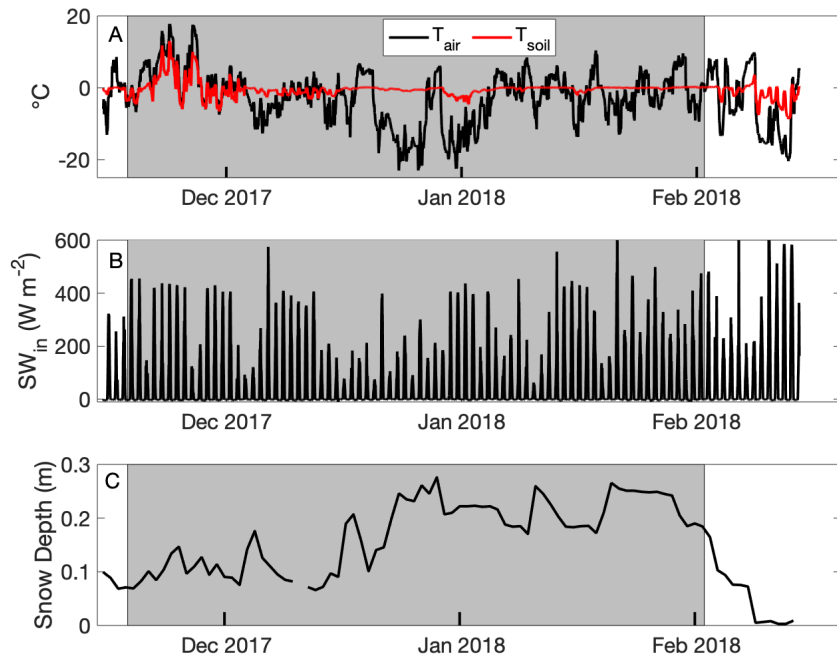


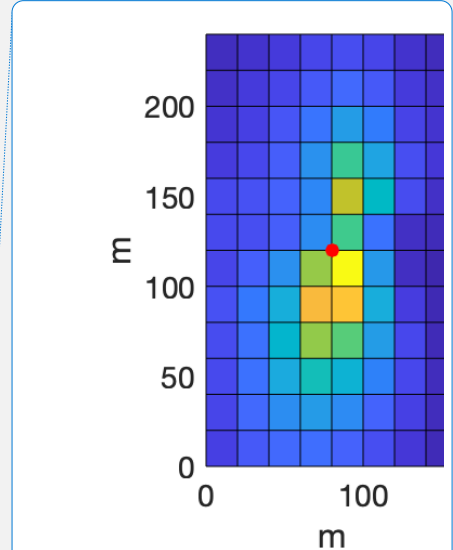
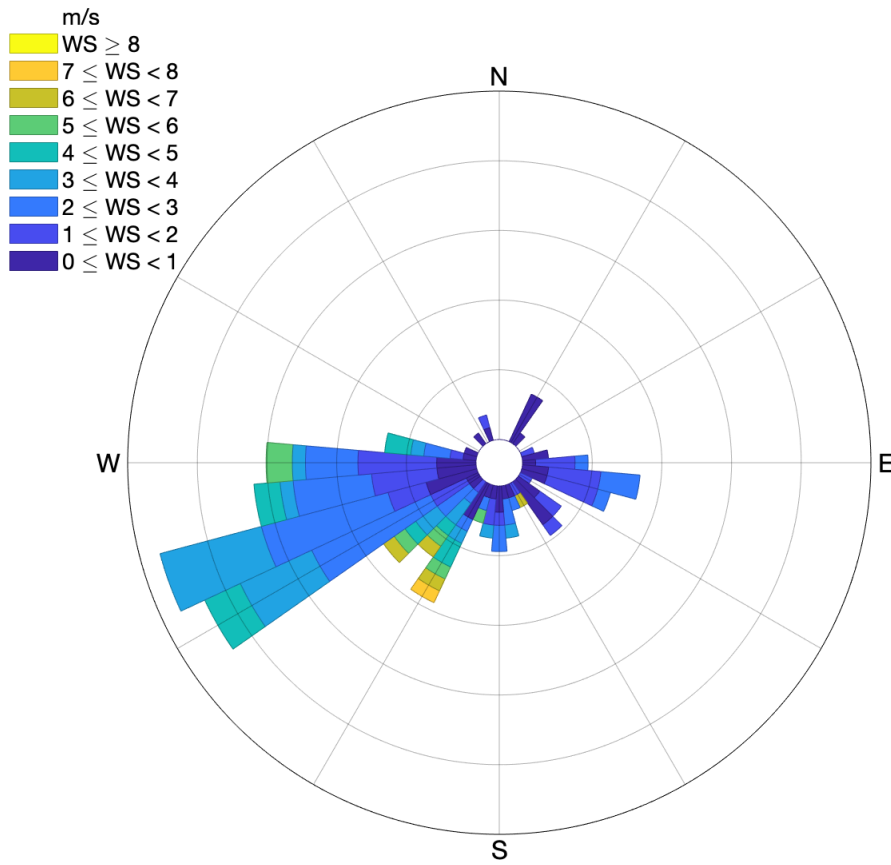
Figure 5: (A) Air (T_{air}) and soil temperature (T_{soil}), (B) incident shortwave radiation (SW_{in}), and (C) snow depth from a micrometeorological tower enclosed within an electric fence on a bison pasture near Gallatin Gateway, Montana, USA. Bison were present in the pasture during the interval bounded by the grey background.

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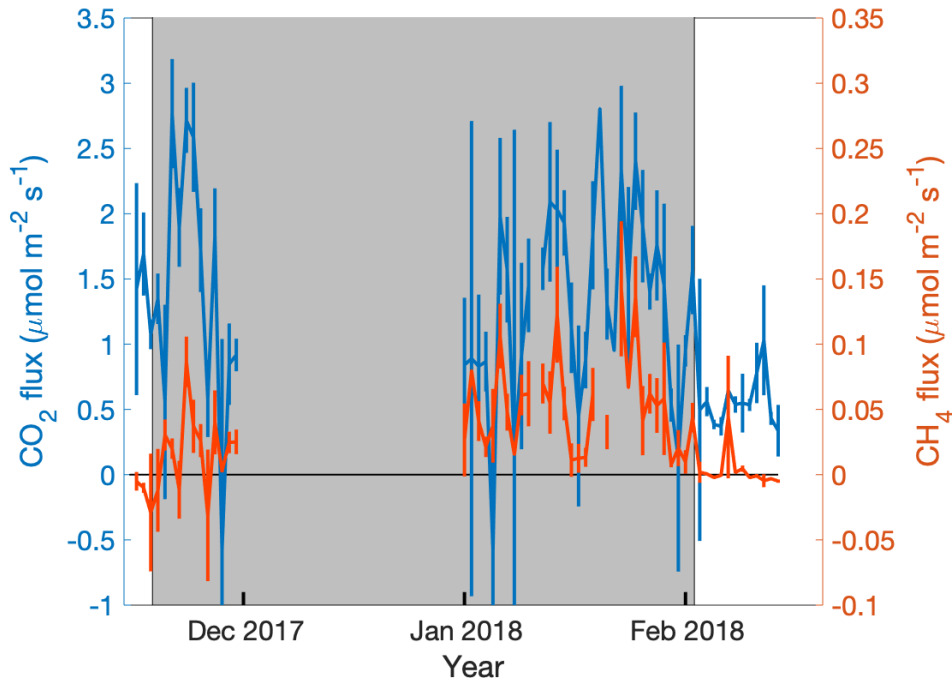
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 Figure 6: The pasture area with the daytime (0700-1700) flux footprint averaged over the entire study period for the 20 m grid demonstrated in Figure 1. The red dot denotes the location of the eddy covariance tower. On average 86% of the footprint area resided within the dimensions of the field during the measurement period.

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845 [Figure 6: A wind rose following Pereira \(2020\) for periods when eddy covariance measurements and bison location measurements were available. WS: wind speed.](#)



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Figure 7: The daily mean and standard error carbon dioxide and methane fluxes with standard error during daytime hours (0700-1700) from a pasture near Gallatin Gateway, MT, USA. The gray background denotes the interval during which bison were present on the study site.

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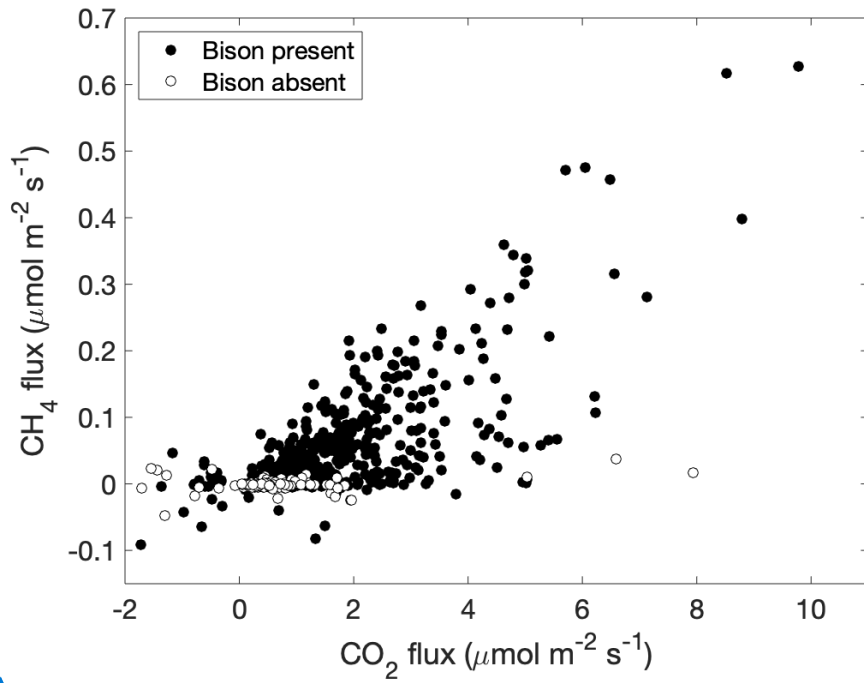
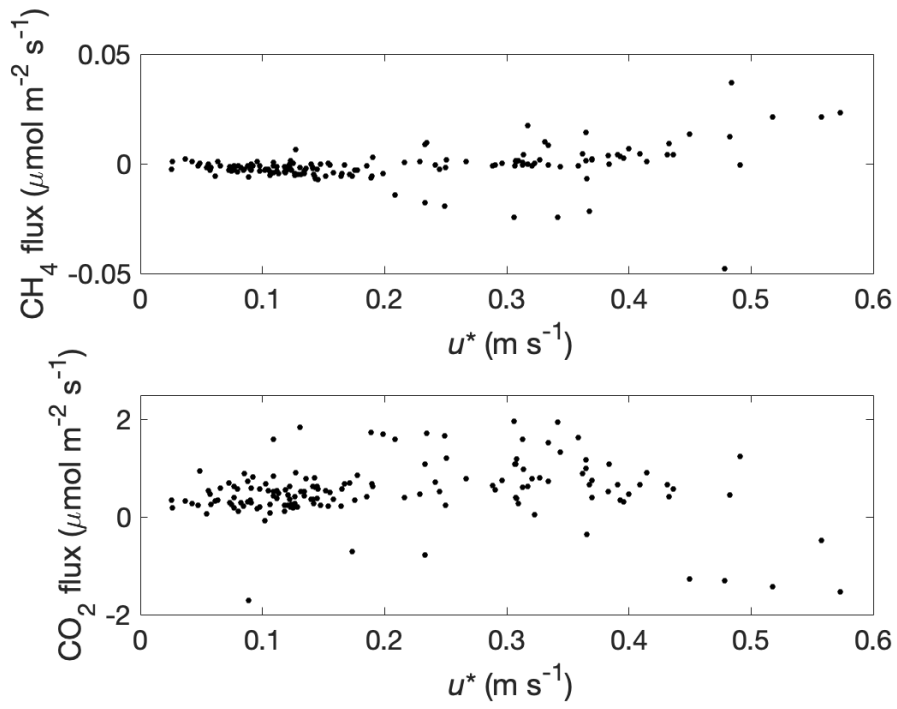
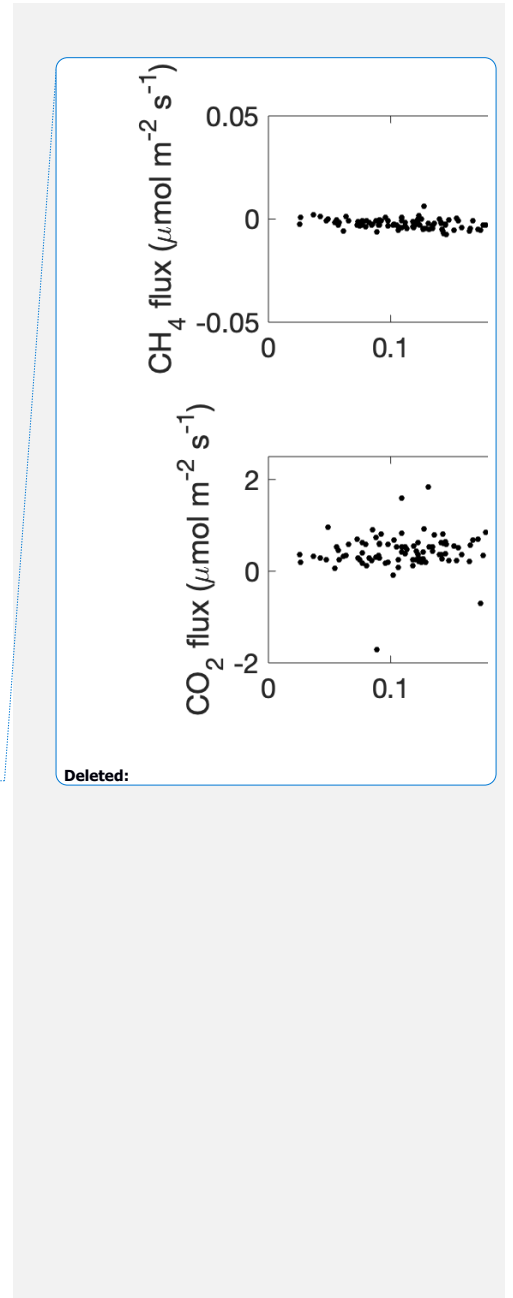
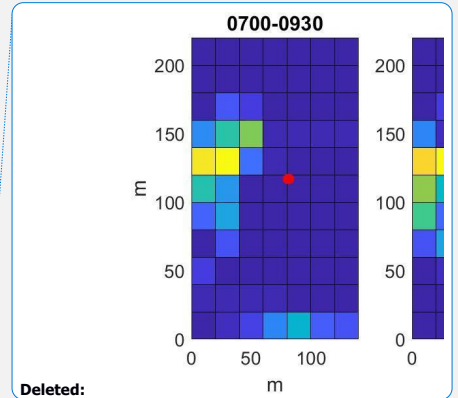
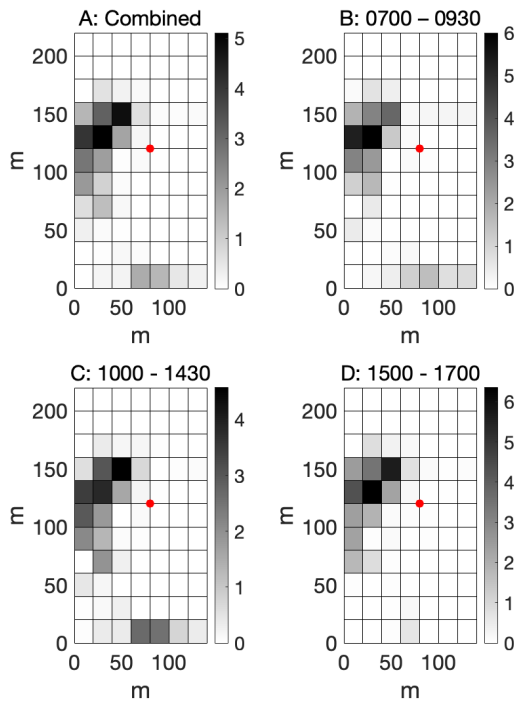


Figure 8: The relationship between carbon dioxide and methane fluxes from the study pasture is shown for periods when bison were present (filled circles) and when bison were absent (open circles).



865 Figure 9: Methane (A) and carbon dioxide (B) fluxes as a function of friction velocity (u^*) when bison were absent from the study pasture.

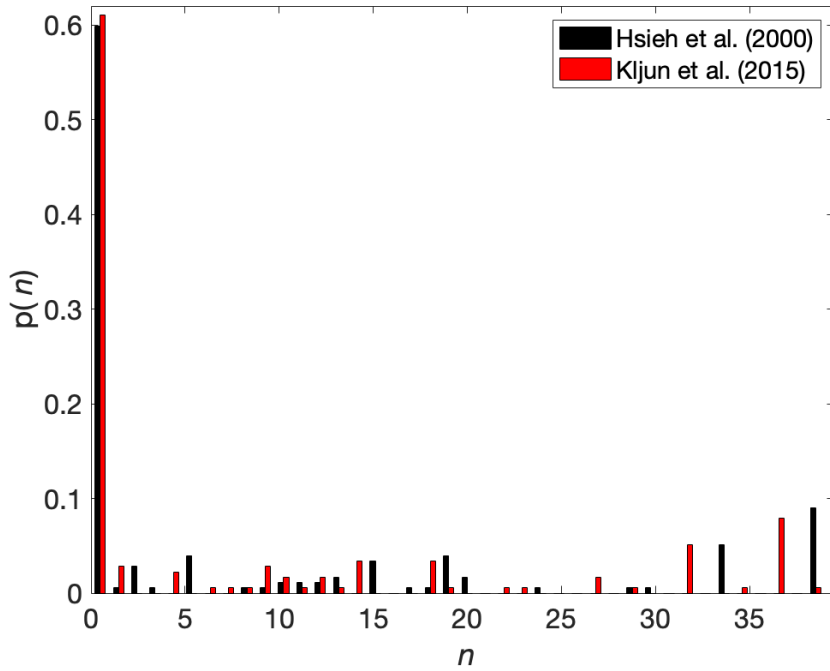




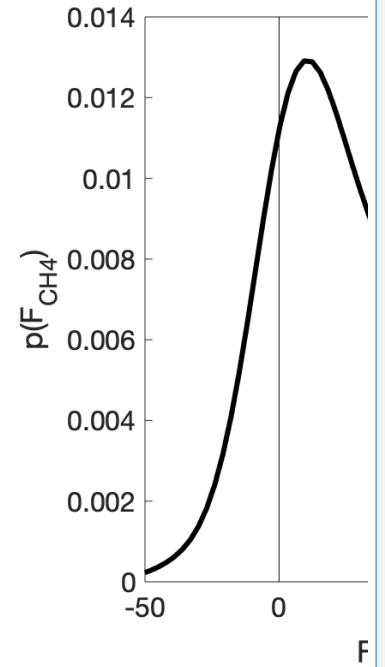
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870 Figure 10: Average proportional bison density for three periods of the day. Each colored pixel represents a 20-meter grid square, red dots denote the location of the eddy covariance tower, and subplot titles refer to local time. Color denotes average proportion of bison present in each grid cell for the 39-animal herd.

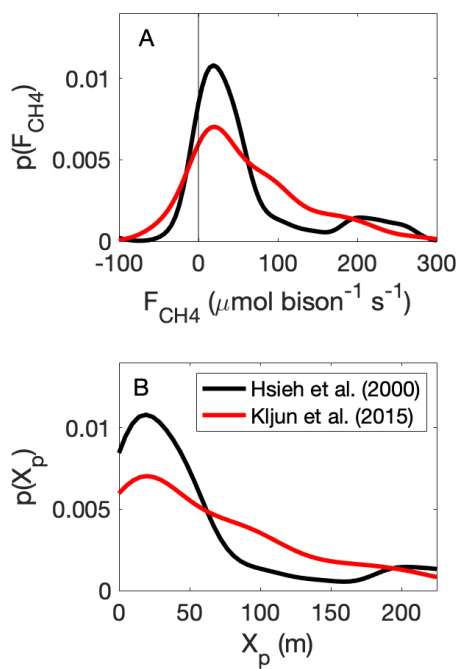
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875 Figure 11: The probability ($p(n)$) of the number of bison (n) in the 90% flux footprint for the Hsieh et al. (2000) and Kljun et al. (2015) footprint models for periods when flux measurements were made and camera imagery was available.



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880 **Figure 11: Kernel density estimates of the distribution (p) of (A) methane efflux (F_{CH_4}) on a per-bison basis and (B) the peak (X_p) of the source-weight function for half-hourly flux footprints derived by the Hsieh et al. (2000) and Kljun et al. (2015) flux footprint models.**

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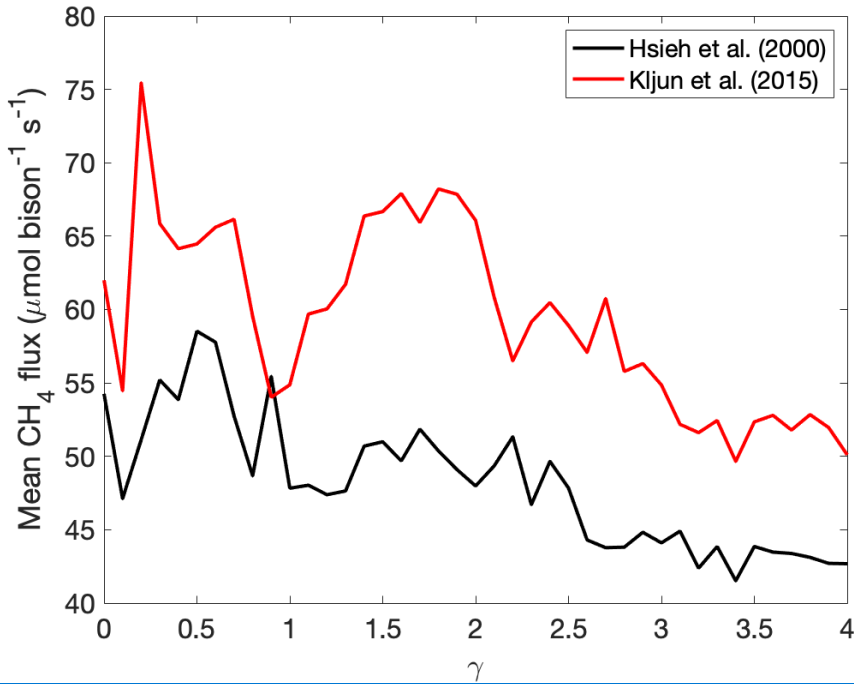
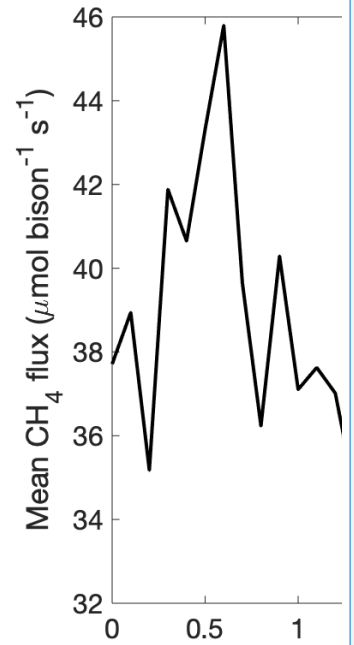


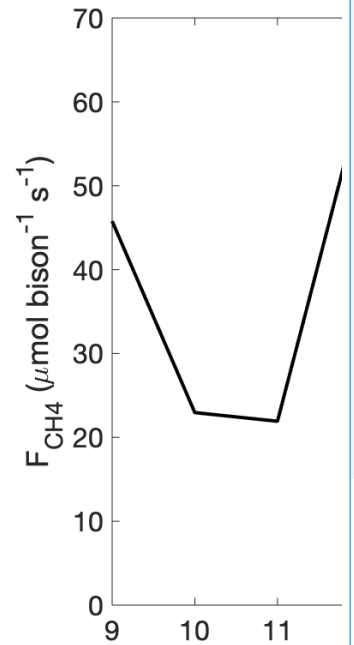
Figure 12: Mean methane efflux on a per-bison basis as a function of spatial smoothing of bison location estimates using the two-dimensional Tikhonov Regularization approach described in Stoy and Quaiñe (2015) for different values of the Lagrange multiplier γ and the footprint models of Hsieh et al. (2000) and Kljun et al. (2015).



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