

MEASURING METHANE EMISSIONS FROM AMERICAN BISON (*Bison bison* L.)
USING EDDY COVARIANCE

by

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ABSTRACT

American bison (*Bison bison* L.) have recovered from the brink of extinction over the past century. Bison offer potential environmental benefits as they re-occupy their native range, but many specific impacts of bison reintroduction are not well understood. Methane emissions are known to be a major climate impact of ruminants, but few measurements for bison exist due to challenges caused by their mobile grazing habits and safety issues associated with direct measurements. Here, we measure the methane and carbon dioxide fluxes from a bison herd on winter range using the eddy covariance technique. Methane emissions were negligible (mean = $0.0024 \mu\text{mol m}^{-2} \text{s}^{-1}$, SD = $0.0102 \mu\text{mol m}^{-2} \text{s}^{-1}$) before and after bison grazed in the area sampled by the eddy covariance flux footprint with the exception of a single spike possibly attributable to thawing soil or the presence of white-tailed deer (*Odocoileus virginianus* Z.). Methane fluxes when bison were present in the study area averaged $0.041 \mu\text{mol m}^{-2} \text{s}^{-1}$ (SD = $0.046 \mu\text{mol m}^{-2} \text{s}^{-1}$), similar to previous measurements over sheep and cattle pastures, but with little diurnal pattern due to a lack of consistent bison movement habits over the course of each day. An eddy covariance flux footprint analysis coupled to bison location estimates from automated camera images calculated methane flux with a median of $56.5 \mu\text{mol s}^{-1}$ per animal and a mean of $91.6 \mu\text{mol s}^{-1}$ per animal, approximately 50 and 75% of established emission rates for range cattle, respectively. Eddy covariance measurements are a promising way to measure methane and carbon dioxide flux from large ruminants on native range and we recommend comparisons amongst alternate grazing systems to help identify management strategies that are cognizant of climate.

CHAPTER ONE

BACKGROUND AND LITERATURE REVIEW

Introduction

Following European colonization of western North America, American bison (*Bison bison* L.) populations were forced to the verge of extinction by pressure from hunting and habitat loss. So extreme was the decimation of the species that the total bison population, thought to number between 30 and 60 million at its precolonial peak (McHugh 1979; Flores 1991), declined to only a few hundred individuals by the turn of the 20th century (Hornaday 1910). In the last century, the coordinated efforts of sovereign Indian tribes, the U.S. federal government, and private landowners have succeeded in growing bison populations to about 500,000 individuals (Freese et al. 2007).

The exceptional resurrection of American bison has spawned decades of interest in their behavior, physiology and ecology. At their precolonial populations, the animals' size and number meant that their presence played an overwhelming role in the entire North American prairie and woodland biomes which comprised much of their range. As prairie ecosystems have endured a 95% reduction in area due to human cultivation (Knapp et al. 1999), the simultaneous increase in bison populations ensures that they once again play a major transformative role in their native and managed ecosystems. Whereas the task of managing bison was formerly a rush to increase their numbers and avoid extinction, their transition to a non-threatened status has brought with it questions

as to their local and regional ecological impacts, as well as their optimal number and distribution.

While bison shape their home ecosystems, their historical effects are known to have extended globally. During the pre-industrial holocene period from 1200-1800 CE, methane emissions from Great Plains bison herds are estimated to have been approximately 3 teragrams per year (Kelliher and Clark 2010; Chappellaz, Fung, and Thompson 1993), which represented one third of global enteric methane emissions at that time. Methane is a significant greenhouse gas, responsible for roughly 20% of the radiative forcing which causes climate change (Etminan et al. 2016), and its atmospheric concentrations are increasing. To understand the dynamics of atmospheric methane, climate scientists are increasingly incentivized to enumerate accurate methane budgets and predictions. As American bison continue their long recovery and their impact on Great Plains ecosystems becomes more significant, understanding the magnitude and dynamics of their methane emissions will be increasingly relevant in regional and global greenhouse gas budgets. Methane efflux from bison is not well characterized, however. Only a single study has directly measured their methane emissions (Galbraith et al. 1998) and, in this instance, the subject animals consisted solely of yearling cows fed alfalfa hay, which is not representative of most bison, especially those in the wild.

Eddy covariance techniques have been successfully employed to assess the methane emissions of several domestic livestock (Felber et al. 2015; Dengel et al. 2011; Prajapati and Santos 2018) using indirect measurements of methane concentrations and air movement. In this thesis, I discuss the application of these same methods to determine

bison-associated methane fluxes in a natural setting.

Literature Review

Bison Management in the Northern United States

At their precolonial peak, American bison ranged from the modern-day Canadian Prairie Provinces – where their territory abutted that of the more northerly wood bison – to northern Mexico (Hornaday and United States National Museum, 1889). The intention of settlers and the U.S. government to curtail indigenous Americans' access to resources and open land for domestic cattle resulted in the rapid decimation of bison populations due to hunting, exotic bovine diseases, and competition with livestock (Flores, 1991). As state and federal governments were not incentivized to take action which could have limited westward expansion, calls to safeguard free-falling bison populations were ignored (Haines and Dary, 1975). Between 1864 and 1872, Montana, Idaho, and Wyoming passed legislation to protect game animals, including bison (Freese et al., 2007), though the states were not adequately equipped to enforce those laws. It was only in 1894 that the administration of President Grover Cleveland enacted protections for the Yellowstone bison herd (Gates 2005). By this point, Yellowstone bison were the sole remaining herd of free-ranging American bison, and even their numbers dropped as low as 23 (Meagher 1973). The 1902 introduction of transplanted bison from Montana's Pablo-Allard herd and Texas' Goodnight herd helped to rebuild Yellowstone bison populations, as did protection by the U.S. Cavalry against rampant poaching (Meagher 1973). Freese and Aune (2007) largely credit private citizens with saving bison from

extinction. Before any protections were enacted at the federal or state levels, individuals had gathered all remaining bison aside from the Yellowstone herd. Private herds included the aforementioned Pablo-Allard and Goodnight herds which were introduced to Yellowstone, and the remainder of the Pablo-Allard herd was purchased by the Canadian government in 1907.

The Yellowstone herd, still the largest public herd in the United States, was actively managed to maximize population growth until shortly after the National Park Service assumed control of the Park in 1918 (National Research Council. 2002. Ecological Dynamics on Yellowstone's Northern Range), at which point overgrazing concerns prompted the adoption of intensive population control policies for both elk (*Cervus canadensis*) and bison. Bison numbers remained suppressed until the release of the pivotal Leopold report (Wildlife Management in the National Parks 1969) which found these measures to be ineffective. This report ushered in a natural regulation policy, which allowed bison populations to increase and fluctuate according to environmental conditions. Bison increased in number from 400 to 4000 between 1969 and 1995 as a result (National Research Council. 2002. Ecological Dynamics on Yellowstone's Northern Range).

While a natural regulation approach to bison management had cultivated larger, more robust herds within Yellowstone National Park; external developments meant that the herds would be constrained by the artificial borders of Yellowstone. Conflicts emerged between bison and domestic cattle in areas adjacent to the park as the United States Department of Agriculture (USDA) Animal and Plant Health Inspection Service

(APHIS) intensified its efforts to eliminate the disease brucellosis from cattle (Baskin 1998). Brucellosis had been present in 15% of US cattle herds when the eradication effort began in 1934; by 1995 fewer than 100 infected herds remained. The near-eradication of the disease thus brought the attention of APHIS to wild reservoirs of the disease, which included elk and the Yellowstone bison herd (Baskin 1998).

Brucellosis results from infection by the bacterium *Brucella abortus* and causes fetal abortions in pregnant cattle (Williams et al. 1993); it is transmissible by contact with infected placental fluids. Infection of domestic cattle by wild bison has not been shown conclusively, however studies on captive animals have shown interspecies transmission to be possible (Baskin 1998), and risk assessments have found the risk of wild bison infecting cattle to be small but nonzero (Cheville et al. 1998). The possibility that this could occur galvanized opposition to bison movement outside of Yellowstone as ranchers in surrounding areas feared that their herds could be harmed, and ranchers throughout Montana and Wyoming worried that brucellosis cases in the greater Yellowstone ecosystem could prompt statewide beef export restrictions. Because of this, a “test and slaughter” policy was enacted wherein bison leaving Yellowstone would be culled and tested for *B. abortus*. This was contentious, but rose to national attention when harsh cold and snow affected the region during the winters of 1996-1997, 2005-2006 and 2007-2008 (Keiter 1997; Kilpatrick et al. 2009); (White et al. 2011). During these years, bison left Yellowstone National Park in large numbers to seek more favorable conditions at lower elevations. As a result, more than 1000 bison were killed during each of those winters.

The large bison slaughter of 1996-1997 prompted drafting of the Interagency

Bison Management Plan (IBMP), which sought to create buffer zones outside Yellowstone National Park for bison which tested negative for *B. abortus* and create a brucellosis vaccination strategy for both cattle and bison (Interagency Bison Management Plan for State of Montana and Yellowstone National Park: Environmental Impact Statement 2000). The IBMP enabled brucella-negative bison to access certain year-round and winter range units which bordered the National Park, each of which was selected to ensure spatial separation of bison and cattle. The IBMP also set research goals for determining the persistence of *B. abortus* in the environment such that a minimum temporal separation of bison and cattle could be established for ranges shared by the two species. The IBMP was adjusted in 2005 and 2006 to incorporate hunting and strategic hazing outside of Yellowstone National Park as management tools.

Importantly, the IBMP also codified expectations for a bison quarantine facility from its outset. Such a facility could help to minimize bison slaughter by containing excess animals when quotas for bison leaving the park had been met (White et al., 2011). The facility was completed by 2005, and 216 bison were sent there between its opening and the end of 2010. As bison leaving Yellowstone National Park continued to exceed exit quotas, it became necessary to devise a contingency plan for bison kept in quarantine. Default plans mandated the slaughter of *B. abortus*-negative bison if quarantine capacity was exceeded, however the Montana Department of Fish, Wildlife and Parks found that the brucellosis status of bison could be determined with certainty in quarantine (Montana Fish, Wildlife and Parks, 2009) and thus suggested that some bison which were found to be brucellosis-free could be transferred to a ranch operated by

Turner Enterprises, Inc. near Bozeman, MT or to Guernsey State Park, WY. Additionally, regional Indian tribes asked to take possession of quarantined bison for purposes of food, conservation and cultural preservation. This resulted in the transfer of bison to tribes such as the Nez Perce and Confederated Salish and Kootenai for slaughter, as well as the transfer of 63 brucellosis-free bison to the Fort Peck Reservation of northeastern Montana for the purposes of establishing conservation and commercial herds. While managers and stakeholders continue to negotiate policies to minimize the slaughter of bison, as well as the interaction of bison and cattle, existing policies continue to function; another shipment of quarantined brucellosis-free bison is slated to arrive at the Fort Peck Reservation's bison range in late 2018 or early 2019.

Indirect Measurements of Animal Methane Emissions

Widely cited methane emission values exist for cattle (Johnson and Johnson 1995; Moe and Tyrrell 1979) as well as most common livestock varieties such as sheep, goats and pigs (Johnson, Ward 1996; Crutzen, Aselmann, and Seiler 1986). These values are often measured using hoods or chambers which allow all intake and eructation of methane to be monitored. While this method provides highly precise measurements which accurately characterize gas fluxes from domesticated animals, often in feedlot or dairy settings, the estimates found may not be representative of animals in their native environments. Work by Moe and Tyrrell (1979) and Johnson and Johnson (1995) described the relationship between feed content and methane emissions such that eructation could be approximated for cattle fed a variety of diets. This has greatly aided the incorporation of ruminants into global methane budgets (Kirschke et al. 2003), yet it

remains difficult to estimate the methane emissions of individual herds, especially when they are grazing on open range. While methane eructation may be measured by traditional methods using gas collection hoods and chambers, this is time consuming and the confinement of animals for measurement may alter their metabolism as they are immobilized and likely stressed. Ideally, the methane emissions of animal herds in realistic environments could be determined without the need for invasive techniques by employing eddy covariance techniques.

Eddy covariance methods employ a combination of elevated three-dimensional anemometers and gas analyzers to measure heat, trace gas, and momentum flux between the land surface and the atmosphere (Baldocchi 2003). The calculation of flux values using eddy covariance data relies on consistent and accurate air movement and gas concentration measurement, as well as thorough mixing of air sampled by instrumentation. Air mixing is quantified by frictional velocity (u^*), which expresses the shear between adjacent layers of moving air.

While eddy covariance measurements enable indirect measurement of gas flux, they must make flux estimates at a distance from their areas of interest, which creates a significant source of uncertainty. For this reason, it is necessary for them to operate for weeks or months at a time, and high-frequency measurements must be averaged, usually over a 30-minute period, though the automation of instruments means that this can be done with little or no human intervention. Because of this, strategically deployed instruments can enable accurate and inexpensive estimation of surface-atmosphere gas fluxes (Baldocchi 2003). By incorporating the locations of livestock, correlating gas

fluxes with animals' presence may allow for practical in situ measurement of livestock methane emission on a per-animal basis.

Eddy covariance instrumentation has been deployed in the presence of livestock on several occasions. In a study which assessed gas analyzer functionality, Detto et al. successfully attributed spikes in methane flux to the presence of cattle in a pasture (Detto et al. 2011). A study on a British sheep pasture found a relationship between the magnitude of methane fluxes and the number of sheep present in the study area (Dengel et al. 2011). These studies incorporated flux footprint modelling, which estimates the source area of that is sampled by the eddy covariance system using measurements of wind speed, direction, and variance, and variables that influence turbulence including u^* , sensible heat flux, and (potential) temperature. By doing so, the fraction of measurements which arise from a given unit of area on the ground during a data averaging period can be determined. By combining footprint models with records of animal distribution during each data averaging period, the magnitude of animal contributions to methane flux measurements could be estimated.

Accurately describing animal distribution at different time points has presented a significant challenge to eddy covariance studies of animal methane emissions. Detto et al. (2011) employed cameras co-located with instrumentation to determine whether cattle were present in their study area. Dengel et al. (2011) placed instrumentation in the vicinity of several sheep pens and relied on knowledge of the number of sheep in each pen, as well as the diurnal movement patterns of sheeps within the pens. Each of these studies successfully isolated a methane flux signature associated with the presence of

animals, but they were unable to precisely quantify the animals present and thus could not calculate methane emissions on a per-head basis.

Work by Detto et al. (2011) and Dengel et al. (2011) greatly advanced prospects for the use of eddy covariance in detecting animal methane emissions by isolating the signature of livestock presence from background methane fluxes. These studies were not, however, able to estimate methane eructation on a per-animal basis due in part to the difficulty of monitoring animal distribution with sufficient resolution. Using insights from these studies, the most rigorous employment of eddy covariance methods to track ruminant methane emissions was carried out by using GPS tracking devices to monitor the locations of each cow in a herd (Felber et al. 2015). This enabled the study authors to combine flux footprint intensity with highly precise cattle density and find a correlation between the density of cattle within the footprint and observed methane flux. This method yielded methane emission values between 282 and 423 g CH₄ day⁻¹. While these estimates are approximately twice as large as widely cited cattle methane emission estimates (EPA, 1993), they provide realistic background values measurements from bison can be compared against.

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CHAPTER TWO

METHANE FLUX FROM AN AMERICAN BISON HERD MEASURED USING
EDDY COVARIANCEIntroduction

The American bison (*Bison bison* L.) was hunted to near extinction during European expansion across North America. In the late 19th Century, fewer than 100 reproductive individuals existed on private ranches in the United States (Hedrick, 2009). The current bison population is approximately 500,000 due to the collective efforts of sovereign Indian tribes, government agencies, and private landowners (Zontek, 2007). As bison have recovered, their ecological role has become better understood and their potential as a livestock species has been explored. With these developments, the task of caring for bison herds has transitioned from rescue to management, wherein bison are treated as a versatile and renewable resource (Gates 2005, Zontek 2007).

Given widespread interest in bison reintroduction, their abundance can be expected to increase, and researchers and land managers will have additional incentive to understand the environmental consequences of their expansion. Recent research has characterized bison behavior in their native habitat, often in contrast to closely-related domestic cattle (*Bos taurus* L.), with which bison can interbreed.

Bison in natural settings tend to alter grazing habits seasonally, searching broadly for the most energy-dense forages in summer months and displaying spatial preference for preferred meadows in the winter (Fortin et al., 2003). They tend to seek forage in

areas which have recently burned (Vinton et al., 1993) and feed preferentially on grasses, enhancing forb diversity as a result (Knapp et al., 1999). Because all ruminants emit methane, largely through eructation, and emission rates in cattle are a strong function of cellulose and hemicellulose (Moe and Tyrrell, 1979), questions arise regarding the amount of methane produced by the grass-dominated and cellulose-rich diet of bison.

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). Between 30 and 40 percent of anthropogenic methane emissions are attributable to enteric fermentation in livestock (Kirschke et al., 2013) and recent studies have revised their gross emissions upward by 11% (Wolf et al., 2017; Beauchemin et al., 2008; Thornton and Herrero, 2010). Predicted 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 cellulose content which would result in an increase in ruminant methane emissions (Lee et al., 2016), all else being equal.

Bison in North America are thought to have been responsible for one third of pre-industrial age enteric methane emissions of 9 Tg year⁻¹ (Thompson et al., 1993; Kelliher and Clark, 2010; Chappellaz et al. 1993; Subak 1994), suggesting that their role in the global methane budget must be understood as their populations increase. The only observations that we are aware of measured one-year old penned female bison fed alfalfa pellets and calculated a methane production of 30 L per kg dry food intake (Galbraith et al., 1998). Methane efflux from bison in their native habitat has not been measured to date, and we assume that this will differ from captive bison fed an unnatural diet. Here,

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

Methods

Study Site and Instrumentation

The study site is a 5.5 hectare pasture grazed by a herd of 42 bison on the Flying D Ranch near Gallatin Gateway, Montana, USA (N 45.557°, W -111.229°). The pasture sits on a floodplain immediately west of the Gallatin River (Figure 1). An embankment approximately three meters high forms the pasture's western border, with a small marsh and stand of mature cottonwood trees providing shelter along this side. The site experiences cold winters, with highs averaging 0 °C and lows averaging -11 °C for the December and January during which the study took place, as measured at Bozeman-Yellowstone International Airport 24 km north-northeast of the site. The area receives about 16 mm of precipitation in December and 14 mm in January, almost entirely as snowfall. Bison consumed a mixture of perennial grasses grown in situ and hay grown in nearby fields, which also consisted of perennial grasses.

All data collected in the course of this study were recorded at a 3 m tall tower located near the center of the study pasture (Figure 1). Meteorological records were averaged and saved to a CR3000 datalogger (Campbell Scientific, Logan, UT, USA) at

30-minute intervals. Soil moisture and temperature were collected using a pair of CS650 probes (Campbell Scientific), while a HFP01 heat flux plate (Hukseflux, Delft, The Netherlands) combined with two type T thermocouples provided soil heat flux measurements. To measure incoming and reflected radiation intensity in infrared and shortwave bands, a NR01 net radiometer system (Hukseflux) was mounted 1.5 meters above ground level. At a height of 1.3 meters, a SR50 sonic distance sensor (Campbell Scientific) was installed to gauge snow depth and air temperature and relative humidity were measured at 2.25 meters using a HMP45C probe (Vaisala, Helsinki Finland).

To measure methane and carbon dioxide flux, we used eddy covariance instrumentation placed at a height of 2 m on the 3 m instrumentation tower shared with the meteorological equipment described above. High-frequency (10 Hz) methane and carbon dioxide concentration measurements were made using an LI-7700 open-path infrared gas analyzer (LI-COR Biosciences, Inc., Lincoln, NE, USA) and LI-7200 closed path infrared gas analyzer (LI-COR Biosciences, Inc.), respectively. Open and closed path methane sensors for eddy covariance have been found to perform similarly in field settings (Detto et al., 2011). We use the atmospheric convention where flux from biosphere to atmosphere is denoted as positive. Three-dimensional wind velocity was measured using a CSAT-3 sonic anemometer (Campbell Scientific, Inc., Logan, UT, USA). This instrument was mounted at an azimuth of 219° and directional components of wind were corrected so that outputs were relative to true north. Measurements began on November 14, 2017, bison entered the pasture on November 17, 2017 and left on February 3, 2018, and measurements continued until February 14, 2018. Measurements

were made during daytime hours, 0700 to 1700 local time, to avoid depleting the battery bank and to ensure sufficient light to estimate bison location using game cameras. Four game cameras (TimelapseCam, Wingscapes, EBSCO Industries, Inc., Birmingham, AL, USA) were mounted to the same tower as the eddy covariance instruments and pointed in cardinal directions, and another two were mounted near the pasture edge, facing the tower. These cameras captured images every five minutes and bison locations were tracked over the course of the study period by generalizing their locations to squares in a 20-meter grid overlaid on the pasture area (Figure 1), which represents the grid size that bison could be confidently attributed to given available observations. We test the sensitivity of these location estimates as described in the Spatial Uncertainty section below. Because the presence of bison 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 footage. Simultaneous flux and photographic data were obtained for the period from January 7, 2018 (DOY 7) to February 13, 2017 (DOY 44) excluding January 10, 2017, when instruments were obstructed by snowfall. Flux data without accompanying game camera footage were obtained for the periods from November 14 through 29, 2017 (DOY 318-333) and December 31, 2017 through January 6, 2018 (DOY 365-6).

Flux Footprint

Gas analyzer and sonic anemometer data collected over the course of this experiment were processed using EddyPro software (LI-COR Biosciences, Lincoln, NE, USA) to calculate fluxes. Spike removal was performed as described by Vickers and

Mahrt (1997), with spike acceptance limited to one percent and a maximum of three consecutive outliers. Spikes were defined as more than 3.5 standard deviations from the mean for carbon dioxide and more than 8 standard deviations from the mean for methane given the expectation of intermittent methane spikes from the bison herd.

The flux footprint was calculated using the semi-empirical approach of Hsieh et al. (2000) extended to two dimensions using the measured vertical variance following Detto and Katul (2006). We performed the footprint analysis on a grid of 1 m pixels and aggregated values to the 20-by-20 m grid to which the bison locations were estimated.

The relative contribution of bison to each half-hourly eddy covariance measurement was calculated by finding the product of the bison population in each grid square and the respective values output by the footprint model. This quantity represented the effective number of animals being measured by instrumentation in a single grid square over a given half-hour period, i.e. a footprint-adjusted bison count. Methane flux was then calculated on a per-grid square basis by multiplying flux per square meter by 400 (the area of each grid cell in square meters). This was then divided by the footprint-adjusted bison count value calculated by timelapse camera observations, giving an estimate of methane flux on a per-bison basis.

Spatial Uncertainty

Because the distribution of bison in the pasture was approximated visually based using 5-minute photographic data and aggregated to half-hourly flux measurement periods, a certain degree of spatial uncertainty was inevitable. To account for this, we first smoothed or aggregated bison location using a Tikhonov Regularization approach

(Stoy and Quaife, 2015). This function smoothed or broadened spikes in bison distribution in depending on a variable called the Lagrange multiplier. Increasing (decreasing) the Lagrange multiplier simulated increased (decreased) spatial spread of bison locations to account for the possibility that bison locations may have been disaggregated (aggregated) from camera-based location estimates. This uncertainty simulation was repeated with different Lagrange multiplier values, and the resulting smoothed distribution matrices were used to repeat the per-bison methane flux calculations to estimate the impacts of spatial uncertainty on per-bison flux estimates.

Next, we simulated bison position uncertainty by realigning the bison and footprint matrices, creating a net shift of 20 meters, or one grid square. This was done to explore the possibility that an observer attempting to quantify the position of bison may tend to err in one particular direction, for example repeatedly perceiving bison as being one square east of their actual position. The flux footprint matrix was shifted in the four cardinal directions and per-bison flux estimates were recalculated in each of those positions; if position approximation errors tended to favor one direction over others, moving the footprint matrix in that direction would ostensibly find a more robust relationship between methane flux and the adjusted bison count. All of our results are subject to simultaneous uncertainties in footprint area and bison location, and we present per-bison flux values using multiple methodologies to constrain the likely per-bison flux.

Results

Meteorology

During the study period, incoming shortwave radiation (SWin) ranged between 100 and 400 W m⁻² during peak daylight hours (1000-1400 hours local time), reflecting shifting cloud cover (Figure 3). Clear conditions were common with the exception of a four-week period beginning in mid-December. Daytime average soil temperatures remained at or below 0 °C and air temperatures, while more variable, were also generally below freezing (Figure 3).

Gas Flux

Eddy covariance instrumentation was operational only during daytime hours and, as a result, turbulence was sufficient to ensure consistent atmospheric mixing. Because no correlation existed between u^* and methane or carbon dioxide, even at very low u^* values (Figure 4), it was decided to forgo the use of a u^* filter.

During the flux measurement period for which bison were present, daytime methane fluxes averaged $0.041 \mu\text{mol m}^{-2} \text{s}^{-1} \pm 0.046 \mu\text{mol m}^{-2} \text{s}^{-1}$ (mean \pm standard deviation). Carbon dioxide fluxes averaged $1.2 \mu\text{mol m}^{-2} \text{s}^{-1} \pm 3.4 \mu\text{mol m}^{-2} \text{s}^{-1}$. Average daytime fluxes of both gases were significantly lower when bison were absent ($p = 0.0047$ for methane, $p = 0.0391$ for CO₂) with a concurrent decrease in standard deviation. Methane flux in the absence of bison averaged $0.0024 \pm 0.0102 \mu\text{mol m}^{-2} \text{s}^{-1}$ while carbon dioxide flux averaged $0.75 \pm 2.8 \mu\text{mol m}^{-2} \text{s}^{-1}$. The magnitude of carbon dioxide fluxes was approximately twenty times greater than that of methane and closely

mirrored spikes and trends in methane flux, especially when bison were present (Figure 4). During the bison grazing period, a distinct positive correlation existed between carbon dioxide and methane fluxes (Figure 6); however methane flux variance dropped sharply once bison were moved to a different pasture and the correlation between carbon dioxide and methane ceased to exist. No diurnal pattern of methane flux was observed (Figure 5).

Bison Distribution Analysis

Timelapse camera footage yielded usable imagery for 445 half-hour periods. Aggregate bison distribution for the entire study period was concentrated in an area on the west side of the pasture (Figure 8). Bison generally occupied the same set of grid squares in a sheltered draw throughout each day (Figure 8). They tended to visit the interior of the pasture north of the tower in mornings and afternoons, and made sporadic mass movements to the southernmost edge of the field near its gate during the morning and midday periods. The grid square approximately 50 meters north-northwest of the tower was the location of a pile of supplemental hay and increases in the frequency of bison appearance there are likely associated with the animals' preferred feeding times after dawn and before dusk. When bison populated the southern grid squares closest to the gate, they usually did so in large numbers comprising 75 to 100 percent of the entire herd and remained there for 1-2 hours. Because photographic data showed that the animals tended to increase their activity in the presence – or possibility of the presence – of humans, we assume that these occasional gatherings were likely in anticipation of a person bringing fresh feed, even if no one was in the area.

Camera and eddy covariance measurements were available during 421 half hourly periods. Adjusted bison counts for each grid cell were calculated and, to avoid skewing results or including implausible data, adjusted counts greater than four or less than 0.01 were disregarded. Excluding values more than twice the interquartile range (IQR= 218 $\mu\text{mol s}^{-1} \text{bison}^{-1}$) above or below the median (56.5 $\mu\text{mol s}^{-1} \text{bison}^{-1}$), per-bison methane emission estimates had a mean of 91.6 $\mu\text{mol s}^{-1} \text{bison}^{-1}$ with a standard deviation of 144 $\mu\text{mol s}^{-1} \text{bison}^{-1}$. The application of Lagrangian smoothing functions resulted in the cumulative bison distributions shown in Figure 11. These distributions were then used to repeat the calculations of flux per bison, and the same IQR filter was applied. Lagrange multipliers of 0.1, 1 and 10 averaged 351, 281, and 251 $\mu\text{mol s}^{-1} \text{bison}^{-1}$ respectively, with standard deviations of 562, 420 and 365 $\mu\text{mol s}^{-1} \text{bison}^{-1}$ in the same order.

Realigning the distribution and footprint grids by sliding the footprint matrix in cardinal directions produced data with similar spreads, thus the same IQR filter was applied and the mean and standard deviation were found. Table 2.1 shows these summary statistics:

Footprint matrix movement	μ ($\mu\text{mol s}^{-1} \text{bison}^{-1}$)	σ ($\mu\text{mol s}^{-1} \text{bison}^{-1}$)
North	114	183
South	137	192
East	113	181
West	111	178

Table 2.1: Summary statistics for per-bison flux analyses performed after shifting the flux footprint matrix 20 meters in the direction indicated by the left column.

Discussion

Because the study pasture was located on a floodplain and abutted a riparian area, cold temperatures helped to ensure that thawing soils did not amplify diel methane emission patterns. Indeed, air temperatures averaged less than 0° C during daytime and soil temperatures climbed above freezing only very briefly. Thus, the observations made in the course of this study are unlikely to have been influenced by spurious background methane emissions. At the beginning and end of the experiment, however, soil temperatures did climb above freezing and may have resulted in spikes in background methane flux. Dengel et al. (2011), whose study took place during a much warmer period, noted increased methane flux during warmer afternoon periods and it is likely that a similar effect existed during thaw periods in this experiment. Of note is a distinct spike following the removal of bison from the study pasture which coincided with warmer soil temperatures and may have also been influenced by the presence of deer, which were seen in timelapse camera imagery feeding on leftover hay. No such soil thaws occurred while bison were grazing, however.

During their presence in the pasture, bison are associated with a distinct methane signature, as shown by the immediate decline and stabilization of methane fluxes following their removal from the study pasture, visible in Figure 2. Further, this signature appears to extend to diel methane flux patterns shown in Figure 3. Figure 6 suggests that the distribution of bison in the study pasture varied from morning to midday and afternoon, however it is difficult to infer from the available data whether they, like cattle, are more active during morning and evening hours (Gregorini 2012).

With bison present, half-hourly methane fluxes closely tracked CO₂ (Figure 4) suggesting a shared source. Once bison were removed from the study pasture, CO₂ fluxes remained somewhat variable while methane fluxes stabilized near zero (Figure 4), implying that bison had been virtually the sole methane source in the vicinity.

Most methane flux values calculated on a per-animal basis were narrowly distributed, but several large outliers skewed this distribution. Because a large majority of values were clustered closely around the median, a 4-IQR filter was used and the resulting distribution had a mean (median) of 91.6 (56.5) $\mu\text{mol s}^{-1} \text{ bison}^{-1}$, which corresponds to an annual emission of 46.2 (28.5) kilograms. Previous estimates of methane emissions from range cattle have been close to 60 kg per year per animal (EPA 1993), some 30 percent larger than the mean value calculated here, noting that our measurements are from winter. There is, however, clear skewness which causes the median flux to be only 60% as large as the mean. There are two likely explanations for this. First, in the presence of large ruminants, it is improbable that soil can serve as enough of a methane sink to maintain net negative fluxes across an entire pasture, especially when the flux footprint is accounted for, thus any large negative per-bison flux estimate is likely to be spurious. Second, because per-grid cell methane fluxes are divided by the adjusted bison count to find emissions per animal, a small bison presence in a grid cell at the edge of the flux forces the denominator toward zero and cause a modest methane pulse to be interpreted as a large emission on a per-animal basis. As a result, it is important to filter data with a high noise-to-signal ratio, as was done by including a 4-IQR outlier threshold and omitting data with an adjusted bison count of less than 0.01.

This was especially important in analyzing data smoothed by Lagrangian multipliers as interpolated bison distributions can assign a tiny fraction of one bison to certain grid squares, meaning the denominator of the bison emission function can become smaller and the emission amplification effect mentioned above can be much more drastic if filters are not used.

Incorporating uncertainty as specified by Lagrange multipliers successfully produced a series of distributions with varying degrees of smoothing. Notably, greater smoothing appeared to cause both means and standard deviations to decrease, and a lack of smoothing had an opposite effect. This is likely a result of the fact that heavily smoothed bison distributions are inherently less variable than un-smoothed ones, but due to their larger spread they cannot pinpoint bison locations (and thus methane sources) to the same degree, likely causing their mean values to be lower. Perhaps surprisingly, though, the original data which was used to perform the Tikhonov Regularization had a much lower mean and standard deviation than any of the smoothed datasets, despite having undergone no such processing. This may suggest that the discreteness of the non-interpolated original data insulated it somewhat from extreme variability.

When the footprint matrix was shifted to search for predominant directional errors, the results of per-bison flux calculations were quite similar to each other; a southward movement was the only realignment which caused a significant increase in bison methane emission estimates relative to un-shifted data ($p= 0.001$). The three other directional shifts yielded very similar results; the differences between those three

combined and the southward shift ($p = 0.06$) and the un-shifted data ($p = 0.04$) were near established significance values.

While attempts to incorporate uncertainty did not point to specific sources of error, previous uses of eddy covariance methods to detect trace gas emissions from cattle suggest that footprint modeling techniques play a large role in the spatial attribution of observed fluxes. Prajapati and Santos (2108), for instance, used established analytical and Lagrangian dispersion models (Kljun et al. 2003) and found that the KM01 analytical model (Kormann and Meixner 2001) predicted flux footprint areas five to six times larger than did an approximation of a Lagrangian dispersion model (which is similar to the footprint model used in this study). It is likely, then, that re-analysis using an alternative procedure for flux footprint estimation could significantly alter estimates of flux on a per-bison basis.

While reconciling different footprint models and refining bison distribution tabulation represent significant obstacles to the broader implementation of eddy covariance methods in determining ruminant methane emissions, repetition of studies similar to this one can help to draw a more robust relationship between calculated per-animal fluxes and the actual magnitude of these emissions.

Conclusion

Eddy covariance presents a promising solution for monitoring mobile point sources of trace gases, such as bison, at a landscape scale with instrumentation that is more practical, less invasive and more compatible with natural conditions than traditional

methods. Here, we have demonstrated the effective employment of these techniques and the acquisition and analysis of useful, realistic data using relatively accessible gas flux modeling techniques. The results of uncertainty simulations suggest that, while flux footprint models vary and special attention must be paid to data filtering, robust conclusions can be reached using these methods. Future increases in the scale and scope of this work will help to calibrate more exacting animal gas flux emission estimates.

Figures

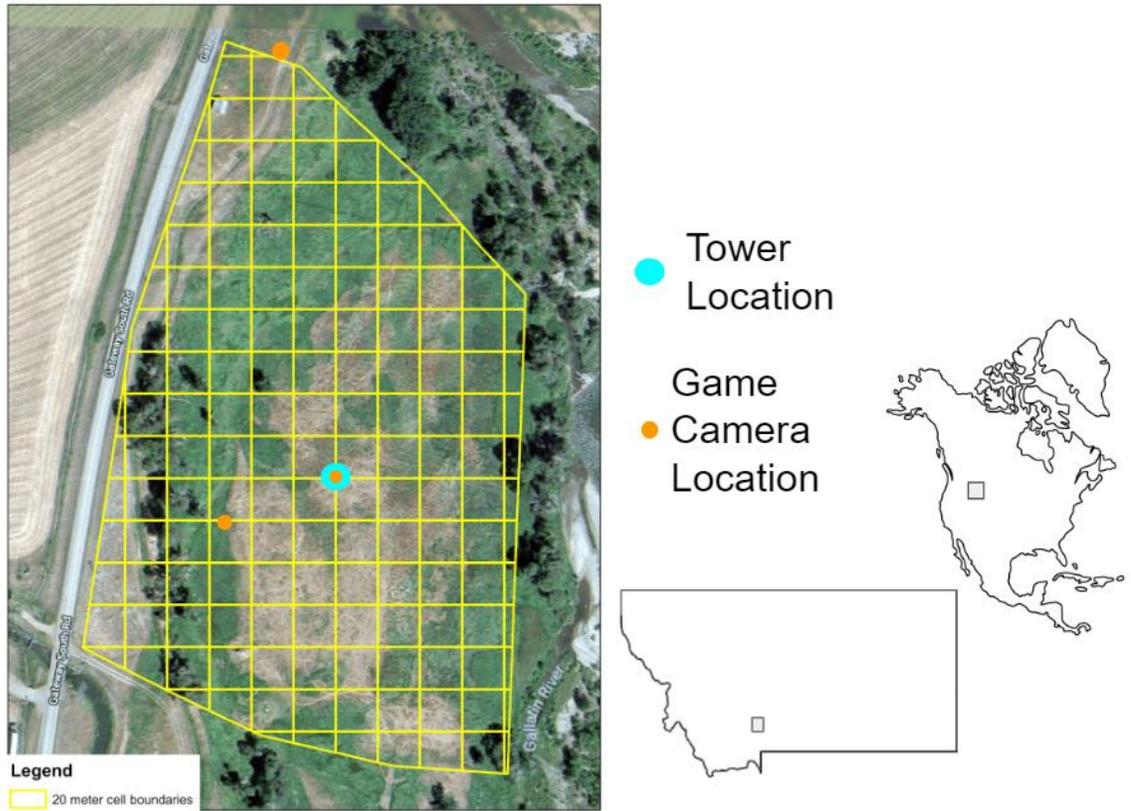


Figure 1: The study pasture near Gallatin Gateway, MT (45.557, -111.229). The 20-meter grid to which bison locations were determined is superimposed in yellow.

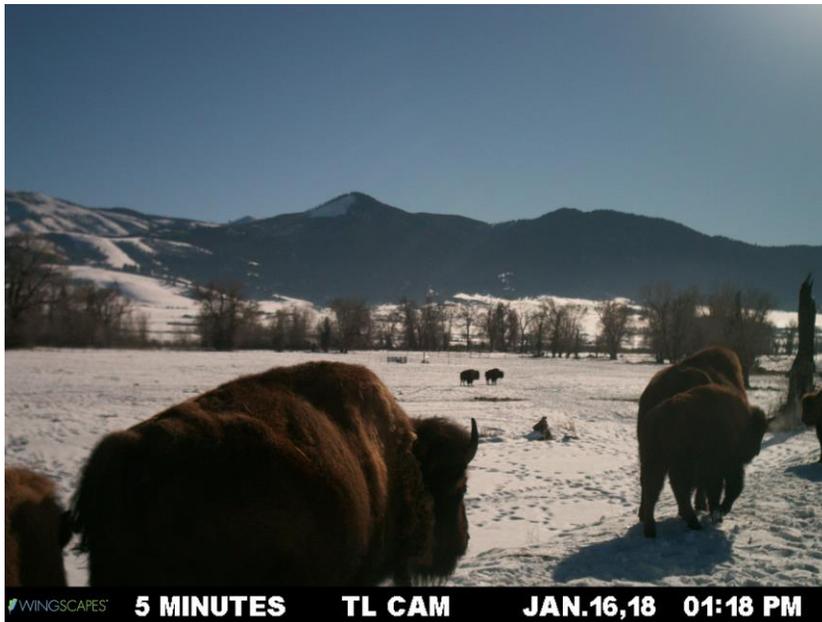


Figure 2: Sample image of bison as viewed from the south-facing timelapse camera. The eddy covariance installation is visible toward the center of the pasture before the row of trees.

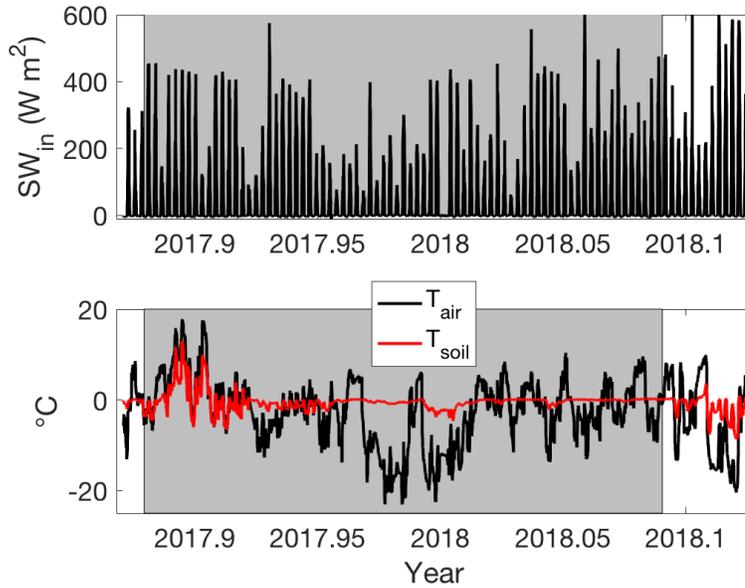


Figure 3: Incident shortwave radiation (SW_{in}), air temperature (T_{air}), and soil temperature (T_{soil}) from the meteorological instrumentation in the study pasture for a period when eddy covariance measurements of methane and carbon dioxide flux were made. Bison were present in the pasture during the interval bounded by the gray background.

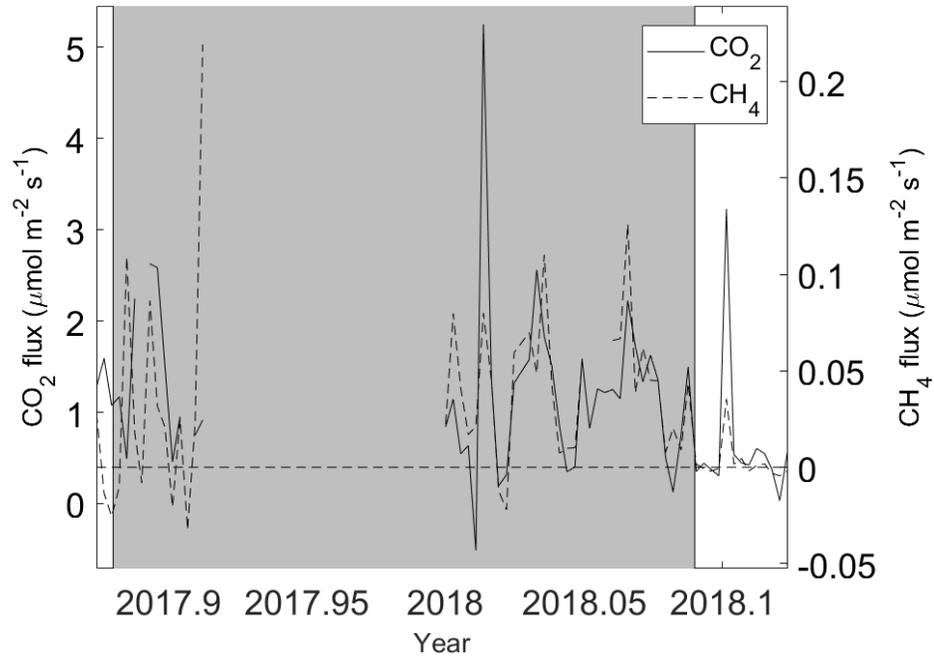


Figure 4: Daily average methane and carbon dioxide fluxes during daytime hours (0800-1700) are shown for the study pasture. The gray background denotes the interval during which bison were present.

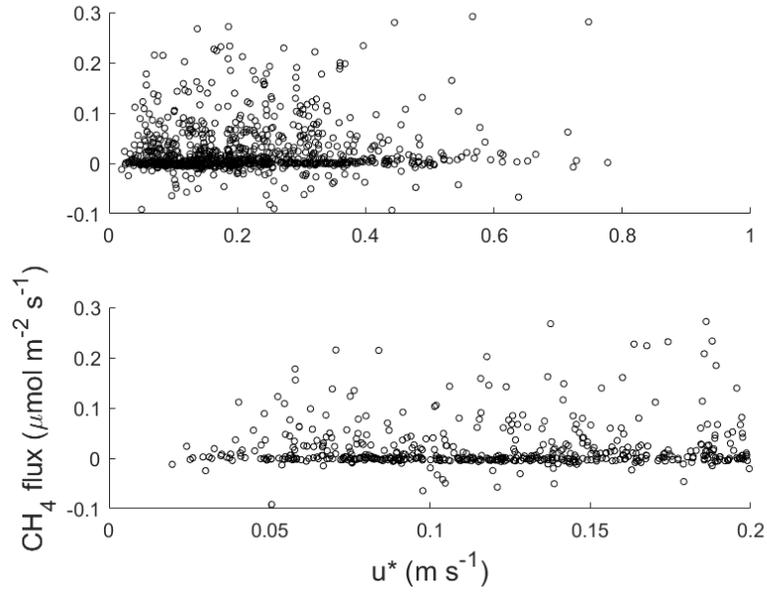


Figure 5: Methane fluxes are compared to frictional velocity (u^*) across the full range of u^* values (top) and the lowest u^* values (bottom).

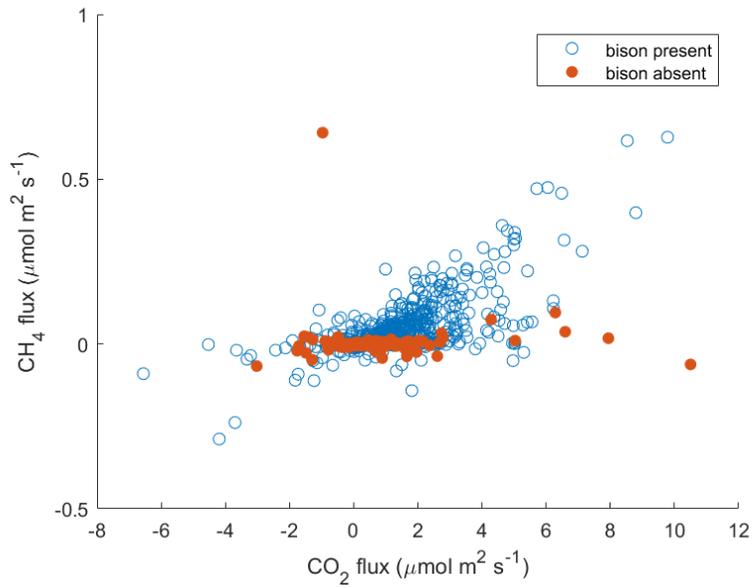


Figure 6: The relationship between carbon dioxide and methane fluxes from the study pasture is shown for periods when bison are present (hollow blue points) and when bison are absent (solid red points).

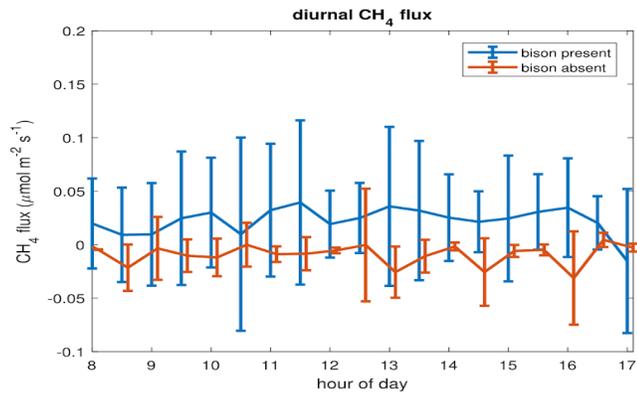


Figure 7: The daily course of eddy covariance-measured methane flux during periods when bison were present and absent from the study pasture during winter 2017/8. Error bars represent one standard deviation.

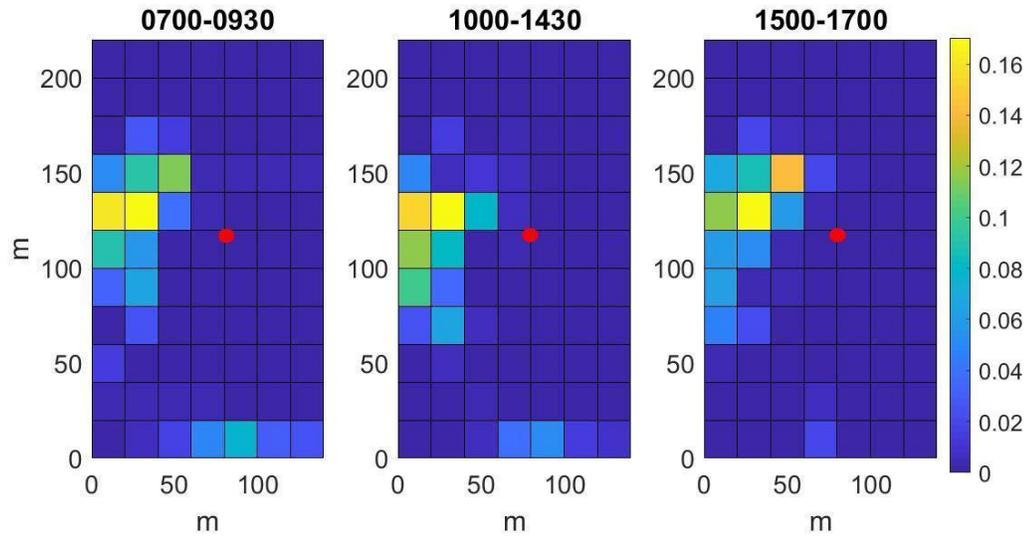


Figure 8: Average proportional bison density is mapped for three periods of the day, showing diurnal movement. Each colored pixel represents a 20-meter grid square; red dots denote the location of the eddy covariance tower. Color denotes average proportion of bison present in each grid cell for the 42 animal herd.

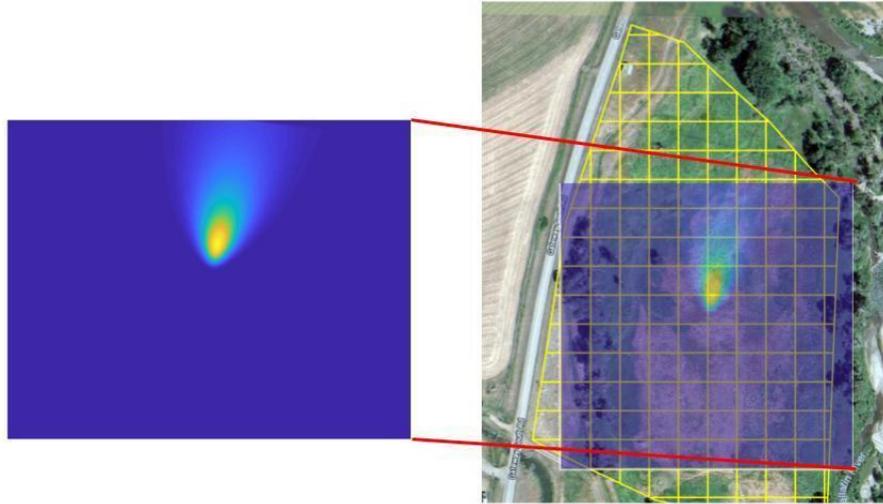


Figure 9: Flux footprint intensity heatmap for a single 30-minute interval is shown superimposed on an aerial photograph of the study pasture with a 20-meter grid overlaid.

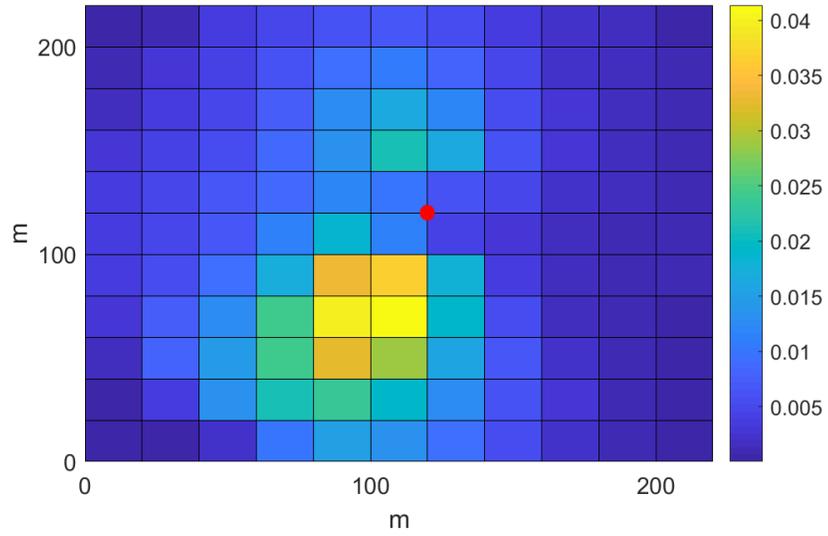


Figure 10: The pasture area is shown with daytime (0700-1700) proportional flux footprint intensity averaged over the entire study period. Yellow indicates areas which frequently fall within the zone sensed by instrumentation; red shows the eddy covariance tower location.

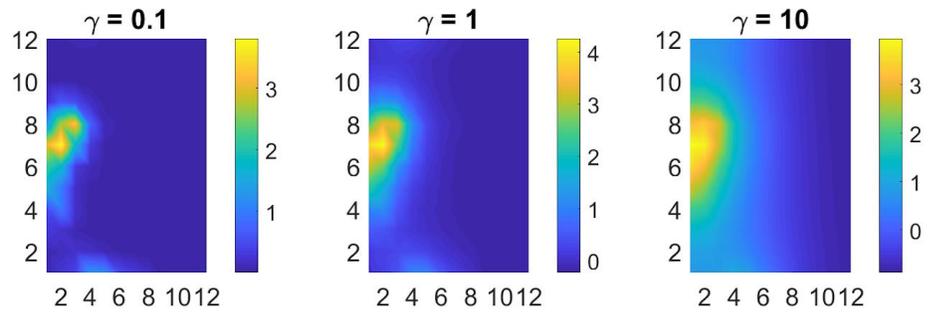


Figure 11: Proportional bison density is shown in three different heatmaps to demonstrate the effect of incorporating uncertainty in location data. The degree of assumed uncertainty was determined by a Lagrange multiplier (γ).

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CHAPTER THREE

SUMMARY OF FINDINGS AND FUTURE RESEARCH

To date, eddy covariance studies of ruminant livestock- such as those by Dengel et al. (2011) and Detto et al. (2011)- have consistently succeeded in detecting the methane signature of animals within their study areas. Here, we demonstrate similar evidence of a distinct methane signature resulting from the presence of bison. Additionally, work by Felber et al. (2015) employed high-precision GPS animal tracking, in addition to flux footprint modelling, to find accurate and realistic estimates of cattle methane emissions on a per-animal basis. Using a herd of 42 bison as a model system, the work presented here achieves similarly realistic results by quantifying animal distribution using pixel-wise resolution of photographic data. Common estimates of cattle methane emissions (EPA 1993) are about half as large as estimates obtained by Felber et al., and 30% larger than estimates for bison found by the study presented here. While the values calculated by this study were closer to directly obtained cattle methane emissions than those calculated by Felber et al., they were considerably more variable. For cows grazing close to instrumentation, Felber et al. calculated a standard deviation of methane emission per animal of 168 g CH₄ day⁻¹, whereas the study presented here calculated a standard deviation of 199 g CH₄ day⁻¹, despite the fact that Felber et al. obtained a much larger estimate of mean methane emissions per animal.

Several factors may explain discrepancies between the results of this study, the estimates by Felber et al. and directly measured cattle methane emissions. Firstly, a

significant difference in methane production may exist between cattle and bison. Additionally, it is likely that, since the resolution of bison distribution analysis was reduced by the photographic methods used, resulting uncertainty caused the standard deviation of methane emission estimates to increase concurrently. Additionally, the uncertainty inherent in assigning bison to pixels based on photographic evidence introduces a source of error as some bison may be misattributed in the process of consolidating photographic data into 20-meter pixel resolution.

While discrepancies persist between estimates of animal methane emissions obtained directly and via eddy covariance methods, the work presented in this thesis demonstrates an increasing degree of accuracy, whereas the closely comparable study by Felber et al. found a highly precise estimate which deviated more from previously established values. The most significant difference between this study and the work by Felber et al. lies in the method of animal distribution quantification; because the Felber study tracked the location of each cow in the study area using GPS devices. This could be expected to give a much more precise estimate of animal population within their instruments' flux footprint area. It stands to reason, then, that repetition of the study described here using tracking methods described by Felber et al. could enable eddy covariance estimates of bison methane emissions which are both accurate and precise.

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