ABSTRACT: The objectives of this analysis were to estimate historic (pre-European settlement) enteric CH$_4$ emissions from wild ruminants in the contiguous United States and compare these with present-day CH$_4$ emissions from farmed ruminants. The analysis included bison, elk (wapiti), and deer (white-tailed and mule). Wild ruminants such as moose, antelope (pronghorn), caribou, and mountain sheep and goat were not included in the analysis because their natural range is mostly outside the contiguous United States or because they have relatively small population sizes. Data for presettlement and present-day population sizes, animal BW, feed intake, and CH$_4$ emission factors were adopted from various sources. Present-day CH$_4$ emissions from livestock were from recent United States Environmental Protection Agency estimates. The most important factor determining CH$_4$ emissions from wild ruminants in the presettlement period was the size of the bison population. Overall, enteric CH$_4$ emissions from bison, elk, and deer in the presettlement period were about 86% (assuming bison population size of 50 million) of the current CH$_4$ emissions from farmed ruminants in the United States. Present-day CH$_4$ emissions from wild ruminants (bison, elk, and deer) were estimated at 0.28 Tg/yr, or 4.3% of the emissions from domestic ruminants. Due to its population size (estimated at 25 million), the white-tailed deer is the most significant present-day wild ruminant contributor to enteric CH$_4$ emissions in the contiguous United States.

Key words: enteric methane, United States, wild ruminant

INTRODUCTION

The environmental impact of livestock production (and agriculture in general) is a matter of continuing national and international public debate (Steinfeld et al., 2006; Capper et al., 2009). Undoubtedly, ruminants are by far the greatest direct source of enteric CH$_4$ emissions from agriculture (US EPA, 2011). Enteric CH$_4$ emissions from horses, for example, are estimated at only about 2.7% of the emissions from beef and dairy cattle (2009 data; US EPA, 2011). Wild ruminants have always inhabited the North American continent, although their population sizes fluctuated dramatically with the westward expansion of European settlers. The bison (*Bison bison*), the elk (or wapiti, *Cervus elaphus*; 4 extant (*C. e. nelsoni, C. e. manitobensis, C. e. roosevelti, and *C. e. nannodes*) and 2 extinct (*C. e. canadensis* and *C. e. merriami*) subspecies in North America; Peek, 2003], or the deer (white-tailed, *Odocoileus virginianus*, or mule, *Odocoileus hemionus*) are some examples of large ruminants inhabiting the continent pre- and post-settlement. Ruminal carbohydrate fermentation pathways are similar between wild and domestic ruminants (Galbraith et al., 1998) and both have been contributing to CH$_4$ emissions in the United States in the past and present. Due to the large size of the bison population in the presettlement period, Kelliher and Clark (2010), for example, concluded that historic bison and contemporary cattle enteric CH$_4$ emissions were similar across the North American Great Plains. To our best knowledge, such estimates for other wild ruminants do not exist. Therefore, the objectives of this study were to 1) propose historic, pre-European settlement (typically, before the 15th century), and contemporary contribution estimates for the major wild ruminant species, bison, elk, and deer, to enteric CH$_4$ emissions in the contiguous United States, and 2) compare these emissions with present-day CH$_4$ emissions from farmed ruminants.

MATERIALS AND METHODS

For this analysis, we used the following formula for estimating annual CH$_4$ emissions from wild ruminants:  
CH$_4$ emissions per unit of DMI (g of CH$_4$/kg of DMI) × DMI (kg/animal/d) × 365 d × species population size. Methane production can be expressed in different ways:

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for example, per animal per day, per unit of feed intake (or as a proportion of), or per unit of energy intake. As clearly shown by Blaxter and Clapperton (1965) in their classic analysis, CH$_4$ production by ruminants is strongly influenced by diet digestibility and level of feed intake, which led the authors to the conclusion that expressing CH$_4$ production on energy intake basis is more informative than expressing it on a DMI (or dietary carbohydrate intake) basis. The current analysis, however, involved so many unknown factors and approximations (population size, DMI) that the difference between using CH$_4$ emission factors based on DMI or energy intake would likely have no measurable effect on our results or conclusions.

For this analysis, low, medium, and high pre-Europe-an settlement bison population size estimates were used (Table 1). The low estimate (30 million) was proposed by McHugh (1972) and was based on the presumed number of animals the available range could support. The high population size (75 million) was based on estimates by the naturalist and writer Ernest Thompson Seton (Dary, 1989). The medium population size in Table 1 (50 million) was an approximate average of the low and high estimates. All bison population estimates are for Plains bison (Bison bison bison); the natural range of the Wood bison (Bison bison athaba-scae) is mostly outside the contiguous United States (i.e., Canada and Alaska; Reynolds et al., 2003) and is not included in this analysis. The average BW of bison was assumed at 638 kg, which is the average BW of Plains male and female bison (Reynolds et al., 2003) assuming a sex ratio of 1:1. Dry matter intake of bison was assumed at 2% of BW, based on DMI of a mature nonpregnant, nonlactating beef cow (NRC, 2000). Two estimates for enteric CH$_4$ emission factor were used to derive the 21 g of CH$_4$/kg of DMI per day emission factor for bison used in Table 1: 1) from Galbraith et al. (1998): 30.1 L of CH$_4$/kg of DMI/d [equivalent factor for bison used in Table 1: 1) from Galbraith et al. (1998): 30.1 L of CH$_4$/kg of DMI/d] [i.e., 10 g of CH$_4$/kg of DMI/d].

As indicated earlier, this analysis did not include important ruminant species such as moose, antelope (pronghorn), caribou, and mountain sheep and goat due to 1) the natural range being mostly outside of the contiguous United States (i.e., Alaska) and in Canada; 2) relatively small population sizes (smaller impact on CH$_4$ emissions), or lack of population size estimates; and 3) a lack of CH$_4$ emission factor estimates.

Present-day population size estimates for bison, elk, and white-tailed and mule deer were from Reynolds et al. (2003), RMEF (2011), Miller et al. (2003), and Mackie et al. (2003), respectively. For consistency, BW, DMI, and CH$_4$ emission factors were as used for the presettlement estimates.

Current estimates for enteric CH$_4$ emissions from farmed ruminants were based on livestock population and emission estimates by US EPA (2011).

RESULTS AND DISCUSSION

Two components are used to estimate greenhouse gas (GHG) emissions from domestic or wild animals: population size and emission factor, which depends mostly on the rumen ecology of the particular species, the size of the animal (i.e., BW), level of feed intake, and type of feed consumed. Intensive research in recent years has produced fairly reliable enteric CH$_4$ emission factors for domestic ruminants, but such information is almost entirely lacking for wild ruminants. For the purposes of this analysis, we collected population data of wild ruminants from various sources and assumed BW, DMI, and emission factors based on existing literature. The extreme variability in these data introduces a large degree of uncertainty in the current emission estimates.

Attempts to quantify CH$_4$ emissions from wild ruminants have been made in the past.Crutzen et al. (1996), for example, estimated that, globally, wild ruminants produce about 0.37 Tg of CH$_4$/yr. McAllister et al. (1996) estimated that wild ruminants (bison, elk, caribou, deer, sheep) in Canada alone produce 0.15 Tg of CH$_4$/yr, or 49 g/(animal/d), a figure close to the 41 g/(animal/d) estimated for deer (various species of deer and caribou) by Crutzen et al. (1986). The current analysis was specifically aimed at estimating enteric CH$_4$ emissions from the major wild ruminant species in the contiguous United States. The challenges in estimating GHG, including enteric CH$_4$, emissions from wild ruminants (or any wild animal) are the lack of knowledge of the population size of the animal and the GHG emission factor (per animal or per unit of feed intake). The uncertainty about emission factors per animal or unit of feed intake is a consequence of uncertainties about 1) the type of feed consumed by the
wild animal, 2) the amount of CH$_4$ produced per unit of feed, and 3) the daily amount of feed consumed. These uncertainties combined make the estimations of CH$_4$ production from wild ruminants only an approximation. For example, in the study that most closely resembled a scientific effort to estimate CH$_4$ emissions from bison, elk, and deer, that of Galbraith et al. (1998), the animals were fed sun-cured alfalfa pellets. This kind of diet is not even close to the natural diet of these species in the wild. In addition, in the Galbraith et al. (1998) study, CH$_4$ production was measured in respiration chambers. The possible effects of confinement in respiration chambers on the behavior and metabolism of wild ruminants are not known.

The analysis we present here is not an exception, and we had to use several assumptions and approximations to be able to compute emissions of wild ruminants for the United States in the past and present. For example, historical population numbers are approximations, at best. Present-day population sizes are known with a much greater degree of certainty, but are still approximations. The most critical assumption in the current analysis is the population size of the bison, by far the largest wild ruminant source of enteric CH$_4$ emissions in North America in the presettlement era. As Table 1 shows, CH$_4$ and CO$_2$ equivalent emission estimates can be about 2.5 times different between the low and high bison population estimates. The estimates of Kelliher and Clark (2010) are based on the low bison population figure. In our opinion, neither the low nor the high bison population estimates are scientifically sound, and therefore, we used the high, low, and an average population size to calculate CH$_4$ emissions. The other important factor for estimating enteric CH$_4$ emissions of the bison, the CH$_4$ emission factor, appears to be more consistent in the literature and is not too different from emission factors for livestock species assumed by US EPA (2011). Using a CH$_4$ emission factor of 6.6% of GE intake reported for bison by Galbraith et al. (1998), Kelliher and Clark (2010) estimated that bison emit on average 72 kg of CH$_4$/ (animal/yr), which is about 21.4 g of CH$_4$/kg of DMI, if the 9.2 kg of DMI figure pro-

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**Table 1.** Pre-European settlement (typically, before the 15th century) and current enteric CH$_4$ emission estimates from wild ruminants in comparison with current emissions from farmed ruminants in the United States

<table>
<thead>
<tr>
<th>Species and period</th>
<th>Population size, million</th>
<th>BW, kg</th>
<th>DMI, kg/(animal/d)</th>
<th>CH$_4$ emission, g/kg of DMI/d</th>
<th>CH$_4$ emission, Tg/yr</th>
<th>CO$_2$ equivalents$^1$ emission, Tg/yr</th>
</tr>
</thead>
<tbody>
<tr>
<td>Wild ruminants, presettlement</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Bison (low)</td>
<td>30$^2$</td>
<td>638$^3$</td>
<td>12.8$^4$</td>
<td>21$^5$</td>
<td>2.93</td>
<td>61.6</td>
</tr>
<tr>
<td>Bison (medium)</td>
<td>50</td>
<td>638</td>
<td>12.8</td>
<td>21</td>
<td>4.89</td>
<td>102.7</td>
</tr>
<tr>
<td>Bison (high)</td>
<td>75</td>
<td>638</td>
<td>12.8</td>
<td>21</td>
<td>7.34</td>
<td>154.0</td>
</tr>
<tr>
<td>Elk (wapiti)</td>
<td>10</td>
<td>270</td>
<td>5.4</td>
<td>16</td>
<td>0.32</td>
<td>6.6</td>
</tr>
<tr>
<td>White-tailed deer</td>
<td>30</td>
<td>80</td>
<td>1.6</td>
<td>10</td>
<td>0.18</td>
<td>3.7</td>
</tr>
<tr>
<td>Mule deer</td>
<td>13</td>
<td>86</td>
<td>1.7</td>
<td>10</td>
<td>0.08</td>
<td>1.7</td>
</tr>
<tr>
<td>CH$_4$ emissions</td>
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<td></td>
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<tr>
<td>Total, low bison$^6$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>3.51</td>
<td>73.6</td>
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<tr>
<td>Total, medium bison</td>
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<td></td>
<td></td>
<td></td>
<td>5.46</td>
<td>114.7</td>
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<tr>
<td>Total, high bison</td>
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<td></td>
<td></td>
<td></td>
<td>7.91</td>
<td>166.1</td>
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<td>Wild ruminants, current</td>
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<td></td>
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<tr>
<td>Bison</td>
<td>0.5$^7$</td>
<td>638$^7$</td>
<td>12.8</td>
<td>21</td>
<td>0.05</td>
<td>1.08</td>
</tr>
<tr>
<td>Elk (wapiti)</td>
<td>1</td>
<td>270</td>
<td>5.4</td>
<td>16</td>
<td>0.03</td>
<td>0.66</td>
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<tr>
<td>White-tailed deer</td>
<td>25</td>
<td>80</td>
<td>1.6</td>
<td>10</td>
<td>0.18</td>
<td>3.68</td>
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<tr>
<td>Mule deer</td>
<td>4</td>
<td>86</td>
<td>1.7</td>
<td>10</td>
<td>0.03</td>
<td>0.53</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.28</td>
<td>5.95</td>
</tr>
<tr>
<td>Contribution, % of US current total$^8$</td>
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<td></td>
<td></td>
<td></td>
<td>4.3</td>
<td>4.3</td>
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<tr>
<td>Farmed ruminants$^9$</td>
<td></td>
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<td></td>
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<tr>
<td>Beef cattle</td>
<td>64.8</td>
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<td></td>
<td></td>
<td>4.74</td>
<td>99.6</td>
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<td>Dairy cattle$^{11}$</td>
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<td></td>
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<td>1.58</td>
<td>33.2</td>
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<tr>
<td>Sheep</td>
<td>5.7</td>
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<td></td>
<td>0.05</td>
<td>1.0</td>
</tr>
<tr>
<td>Goats</td>
<td>3.1</td>
<td></td>
<td></td>
<td></td>
<td>0.02</td>
<td>0.3</td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>6.39</td>
<td>134.1</td>
</tr>
</tbody>
</table>

$^1$The global warming potential of CH$_4$ is assumed to be 21 times greater than CO$_2$ (100-yr time horizon; US EPA, 2011).
$^2$See Materials and Methods for population size assumptions.
$^3$See Materials and Methods for BW assumptions.
$^4$Assumed 2% of BW; see Materials and Methods for details.
$^5$See Materials and Methods for CH$_4$ emission factor assumptions.
$^6$Based on the 3 different assumptions for bison population size.
$^7$For consistency, BW, DMI, and CH$_4$ emission factors were as used for the presettlement estimates.
$^8$Current contribution of wild ruminants to the total CH$_4$ (and CO$_2$ equivalent) emissions in the United States [total current CH$_4$ emissions from wild ruminants ÷ (total CH$_4$ emissions from farmed ruminants + total current CH$_4$ emissions from wild ruminants) × 100].
$^{10}$Includes bulls, beef cows, beef replacements, steer and heifer stockers, and feedlot cattle.
$^{11}$Includes dairy cows and dairy replacements.
posed by the latter authors is used. This emission factor is slightly less than the average [91.5 kg/(animal/yr)] of the CH$_4$ emission factors assumed by US EPA (2011) for dairy cows [140 kg/(animal/yr)] and feedlot cattle [43 kg/(animal/yr)], but similar to the emission factor for dairy cows estimated on a DMI basis (19.2 g/kg; assuming 20 kg/d of DMI).

Another critically important factor for estimating enteric CH$_4$ production is feed (or feed DMI) intake. As indicated earlier, for all species DMI was assumed to be 2% of the BW of the animal. This assumed intake, 12.8 kg/d in the case of bison, was greater than the 7.7 kg of DMI/(animal/d) published by Galbraith et al. (1998; bison in captivity, fed alfalfa hay pellets) and the 9.2 kg of DMI/(animal/d) figure estimated by Kelliher and Clark (2010). The Kelliher and Clark (2010) average DMI estimate (2.2% of BW) is close to our assumption, but these authors assumed average, herd-weighted BW of bison of 441 kg, which is less than the 638 kg used in the current analysis [average BW of a Plains male and female bison reported by Reynolds et al. (2003)]. The 2% of BW DMI for elk (5.4 kg/d) is less than the calculated DMI based on 87 g of DMI/(kg of BW$^{0.75}$/d) reported for elk with an average BW of 151 kg by Galbraith et al. (1998). Similarly, DMI for deer used in the current analysis was about 25% less compared with DMI for white-tailed deer with average BW of 34 kg reported by Galbraith et al. (1998).

The Intergovernmental Panel on Climate Change assumed enteric CH$_4$ emission factor for only one wild ruminant species, deer, of 20 kg/(animal/yr) (both developed and developing countries; IPCC, 2006), which is considerably greater than our estimate of 5.8 (white-tailed) and 6.2 (mule deer) kg/(animal/yr) (based on data from Table 1). The IPCC (2006) emission factor is based on New Zealand data by Clark et al. (2003; the report could not be accessed on October 5, 2011) for red deer (i.e., the wapiti in North America; C. elaphus; Fennessy et al., 1981), which is a considerably larger subspecies compared with the white-tailed deer [IPCC (2006) assumes BW for “deer” of 120 kg]. In addition to the larger body size, the IPCC (2006) estimates are based on a greater emission factor per unit of feed intake (21.25 g of CH$_4$/kg of DMI; an average of the adult cow and adult ewe value; New Zealand Ministry of the Environment, 2011), compared with the current analysis and that of Galbraith et al. (1998). The CH$_4$ emission factors assumed in the current analysis are in agreement with Galbraith et al. (1998), who concluded that per unit of feed intake, CH$_4$ emission is greater in bison (and elk) than in deer.

As apparent from Table 1, the bison was by far the most important wild ruminant CH$_4$ emission source in the presettlement period. The size of the animal, its greater DMI, and its sheer numbers were determining its role as the most significant wild ruminant CH$_4$ emitter in that period. Because the bison presettlement population size estimates vastly differ between sources (see Reynolds et al., 2003), we calculated emissions for 3 different scenarios. In all cases, the bison CH$_4$ emissions represented between 84 and 93% of all emissions from wild ruminants in the presettlement period. Kelliher and Clark (2010) concluded that CH$_4$ emissions from bison in the 10 states encompassing the historical range of this animal were close to the present-day CH$_4$ emissions from cattle in these states (2.2 vs. 2.5 Tg of CH$_4$/yr, respectively). It has to be pointed out that our bison population (Plains bison) estimates included bison in the Canadian Prairie Provinces (Alberta, Saskatchewan, and Manitoba), which would likely overestimate CH$_4$ emission for the contiguous United States. According to the distribution map of Reynolds et al. (2003), however, the Canadian portion of the plains bison range was relatively small compared with the distribution range of this subspecies in the contiguous United States. The bison can be considered a migratory animal. As pointed out by Reynolds et al. (2003), in winter, herds, particularly from the northern territories, migrated south in search of more favorable habitats. Migration from higher to lower elevations with approaching winter is also common for the species (Reynolds et al., 2003). To what extent these migratory patterns would have affected the current enteric CH$_4$ emission estimates for the Plains bison is unknown. Further, our emission estimates are on an annual basis. It is likely, however, that emissions varied greatly with type, quality, and availability of pasture throughout the year. The inverse relationship between feed intake (and passage rate) and digestibility is well established in domestic ruminants (Robertson and Van Soest, 1975) and decreased intake of likely less digestible feed during the winter months would have resulted in greater CH$_4$ production per unit of DMI, compared with intake of more digestible pasture in the summer months. This relationship was specified by Blaxter and Clapperton (1965), who noted that increased intake of low-digestibility diets will likely have no effect on CH$_4$ production (per unit of DMI), whereas increased intake of greater-digestibility diets would decrease emissions per unit of DMI. Thus, Galbraith et al. (1998) concluded that DMI of bison, elk, and deer is greater in spring than winter, and Rutley and Hudson (2000) reported a dramatic decline in DM digestibility of winter (32%) compared with summer (69%) pasture for free-grazing bison in Canada. A detailed analysis of the migratory and feeding habits of the bison can be found in Reynolds et al. (2003). These factors have not been considered in the present analysis, but an effort to include them would be very speculative and would likely bring more variability than accuracy to the estimates for bison in Table 1.

Overall, CH$_4$ emissions from bison, elk, and deer in the presettlement period in the contiguous United States were about 86% (medium bison population size) of the current CH$_4$ emissions from farmed ruminants in the United States (Table 1). If the high bison population estimate is considered for this comparison, wild ruminants in the presettlement period emitted about
23% more CH₄ from enteric fermentation than the current domestic ruminants in the United States.

Present-day livestock CH₄ emissions are primarily from cattle; the contribution of sheep and goats to the total emissions is negligible (about 1%; Table 1). Estimates for CH₄ emissions from horses (0.17 Tg/yr) and swine (about 0.10 Tg/yr) were published by the US EPA (2011), but are not included in this analysis. It is worth mentioning that in this most recent US EPA report (US EPA, 2011), GHG emissions from agriculture made up about 6.3% of the total GHG emissions (CO₂, CH₄, N₂O, hydrofluorocarbons, perfluorocarbons, and sulfur hexafluoride) in the United States for 2009 (419.3 vs. 6,633.2 Tg of CO₂ equivalents/yr, respectively). Methane from enteric fermentation was 139.8 Tg of CO₂ equivalents/yr, representing 20% of total CH₄ emissions in the United States, but only 2.1% of the national GHG emissions for 2009. Present-day CH₄ emissions from bison, elk, and deer were estimated at 0.28 Tg/yr, which is 4.3% of the emissions from domestic ruminants. With a population size estimated at 25 million (Miller et al., 2003), the white-tailed deer is the largest present-day wild ruminant contributor to enteric CH₄ (and GHG) emissions in the contiguous United States, contributing 62% of the total emissions from wild ruminants.

In conclusion, historic, presettlement, enteric CH₄ emissions from bison, elk, and deer in the contiguous United States were estimated at 86% of current emissions of farmed ruminants if a bison population size figure of 50 million was used. By far, bison was the largest enteric CH₄ emitter during this period. These estimates have to be interpreted with caution due to the lack of reliable data of population size, feed intake (and composition), and enteric CH₄ emission factors of wild ruminants. Present-day enteric CH₄ emissions from wild ruminants (bison, elk, and deer) represent a relatively small fraction of emissions of farmed ruminants in the United States.

LITERATURE CITED


