Meta-analysis of rumination behavior and its relationship with milk and milk fat production, rumen pH, and total-tract digestibility in lactating dairy cows

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ABSTRACT

Time spent ruminating is affected by diet and affects the rumen environment. The objective of the current study was to conduct a meta-regression to characterize the variation in rumination time and its relationship with milk and milk fat yields and variables mechanistically associated with milk fat synthesis, including rumen pH and total-tract digestibility. The analysis included 130 journal articles published between 1986 and 2018 that reported 479 treatment means from lactating Holsteins cows during established lactation. Milk yield averaged 34.3 kg/d (range 14.2–52.1 kg/d), milk fat averaged 3.47% (range 2.20–4.60%), and rumen pH averaged 6.1 (range 5.3–7.0). Rumination observation systems were categorized into 6 groups, but there was little difference in average rumination time among systems. The total time spent ruminating averaged 444 min/d (range 151–638 d) and occurred in 13.8 bouts/d (range 7.8–17.4 bouts/d) that averaged 32.7 min (range 20.0–48.1 min). Bivariate regressions were modeled to include the random effect of study, and correlations were evaluated through the partial R^2 that excluded variation accounted for by the random effect. Rumination time was quadratically increased with increasing milk fat yield (partial $R^2 = 0.27$) and milk fat percent (partial $R^2 = 0.17$). Rumination was also increased with increasing milk yield, dry matter intake, and rumen pH, and was quadratically related to dietary neutral detergent fiber (NDF) and total-tract NDF digestibility (partial $R^2 = 0.10$ – 0.27). Similar relationships were observed for rumination per unit of dry matter and NDF intake. The best-fit multivariate model predicting total rumination time included milk yield, milk fat yield, and concentration and accounted for 37% of the variation. Total-tract digestibility was available for 217 treatment

means; when included in the model, the partial R^2 increased to 0.41. Last, principal component analysis was conducted to explore the relationship among variables. The first 2 principal components in the broad analyses explained 36.7% of the 39 variables evaluated, which included rumination bouts and time spent ruminating. In conclusion, rumination time was related to milk fat across a large number of studies, although it explained only a limited amount of the variation in milk fat.

Key words: milk fat depression, chewing activity, meta-regression, rumen pH

INTRODUCTION

Milk is an important component of the diets of approximately 6 billion people worldwide (FAO, 2012). Ruminants are effective at digesting human inedible and low-quality feeds and converting them to high value food, but optimal rumen function is essential to animal health, milk production, and feed efficiency. Additionally, milk fat is a major part of the energy value of milk, important to the production of many dairy products, and is highly affected by modifications of rumen fermentation (Bauman and Griinari, 2001; Bauman et al., 2006).

Rumination is the rhythmic regurgitation and remastication of rumen digesta that occurs between meals and during rest periods, especially at night, and it is a key part of rumen function that is readily observable (Allen, 1997; Beauchemin 2018). The goal of rumination is to break apart large particles to increase microbial attachment and digestion and allow passage from the rumen. Saliva flow is also increased during rumination and provides important buffers to increase rumen pH (Beauchemin, 2018). Regulation of rumination is complex and has been correlated with forage NDF level and diet particle size (Allen, 1997). However, associations with milk and milk fat production have not been well characterized.

Activity and rumination monitoring systems are growing in popularity, but their on-farm applications are mostly focused on management of reproduction

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and health (Sjostrom et al., 2016). On-farm rumination observation could also aid nutritional management and optimization of milk and milk fat yield and rumen digestion, but information is lacking on the expected variation in rumination time and the relationship between rumination and milk fat concentration. Rumination has been investigated in many individual studies (Dado and Allen, 1994; Ramirez Ramirez et al., 2016; Fustini et al., 2017). Meta-analysis methods allow aggregation of the results, which improves the ability to detect relationships and explore sources of variation.

The overarching objective of the current study was to conduct a meta-regression analysis to better understand the relationship between rumination behavior and milk and milk fat yield in addition to variables mechanistically related to milk fat including rumen pH and NDF digestion. The first objective was to benchmark expected rumination time and behavior and the variation of these parameters across diverse diets and conditions. The second objective was to understand the relationship between rumination behavior and the variables of interest using both bivariate and multivariate regression. The hypothesis was that increasing rumination time would be associated with increased rumen pH and milk fat yield.

MATERIALS AND METHODS

Collection of Papers

A data set was constructed from peer-reviewed journal articles published in English. First, papers were identified through a literature search using online manuscript retrieval databases [PubMed (<https://www.ncbi.nlm.nih.gov/pubmed>), Google Scholar (<http://www.scholar.google.com/>), ScienceDirect (<http://www.sciencedirect.com/>), and Journal Dairy of Science (<http://www.journalofdairyscience.org/>)] using key word searches. Approximately 600 publications were retrieved using search terms “ruminating time” and “dairy cow.” Second, an author search was conducted for investigators known to publish rumination data (M. Allen, L. Armentano, K. Beauchemin, T. DeVries, R. Grant, and M. von Keyserlingk). Last, papers reported in the meta-analysis focusing on physical effective fiber and rumination by White et al. (2017) were collected.

Inclusion and Exclusion Criteria

The literature search identified articles published between 1986 and 2018. Of the retrieved articles, 156 articles investigated lactating Holstein cows and reported numerical results for rumination time. Studies were

excluded during preliminary data analysis as follows: 4 studies that used breeds other than Holsteins, 6 studies that used nonlactating or transition-period cows (<14 DIM), 2 studies that investigated diets with very low dietary fiber (<15% NDF), 4 studies that had no dietary treatment (e.g., investigated pest flies, genetic, parity, infusion), and 6 studies that were considered statistical outliers with studentized residual outside of ± 3.5 in a distribution analysis (JMP 12.0; SAS Institute Inc.). The final data set included treatment means from 130 papers.

Data Extraction and Categorization

Of the 130 peer-reviewed papers, a total of 94 reported diet composition, 98 reported milk yield and milk fat concentration, and 116 reported the variance of rumination. Data recorded for each treatment, if reported, included diet composition [DM, OM, NDF, starch, CP, ether extract, total fatty acids (**FA**) and physically effective NDF (**peNDF**)]; intakes of DM, NDF, and forage; milk yield and composition; rumination metrics (min/d, min/kg of DM intake, min/kg of NDF intake, min/kg of forage NDF, bout/d, bout length); rumen pH; and total-tract (**TT**) digestibility of DM and NDF. Total NDF intake was recorded as reported for papers specifically reporting the value in their tables and also calculated based on DMI and diet composition for all papers. “Reported” and “calculated” NDF intake were analyzed as 2 separate variables. The number of replicates and variances (SEM or SD) were extracted for total rumination time (min/d) for weighting as described below (St-Pierre, 2001; Sauviant et al., 2008). References for the complete data set are available online (Supplemental File S1; <https://scholarsphere.psu.edu/resources/c1d0ed45-273c-4f9a-a2fd-a8109a84a66b>).

Rumination was measured by diverse methods across the papers. The observation systems used to measure rumination was recorded and classified into 6 categories according to the following criteria:

- Visual observation (**VO**): Feeding and rumination behavior obtained by visual observation every 1, 5, or 10 min over a total of 24 or 48 h. This included human observation of video recordings.
- Beauchemin 1989: Feeding and rumination behavior obtained by an automated system composed of a transducer attached to a leather halter that transformed jaw movements into electrical signals as described in Beauchemin et al. (1989).
- Dado 1993: Feeding and rumination behavior observed by an automated system that used a pres-

sure sensor in a pneumatic nosepiece attached to a halter and feed bins hanging from a load monitor as described by Dado and Allen (1993).

- AJAWS: Feeding and rumination based on jaw movement including pneumatic systems attached to a cord under the jaw (Deswysen et al., 1987), small balloon filled with foam rubber under the jaws (Brun et al., 1984; Tafaj et al., 2005), leather automatic halters with a piezo disk (DeVries et al., 2003), automatic halters that measured mouth movements (Girard and Labonte, 1993), and the Graze Jaw Movement Analysis Software system (IGER; Rutter et al., 1997).
- SCR: Feeding and rumination behavior obtained by a microphone-based monitoring system (SCR Engineers Ltd.).
- Other auto: Feeding and rumination behavior obtained by sensors that could not be grouped in the above categories.

Observation systems were further simplified into 2 categories of all VO and all automated observation systems.

Statistical Analyses

Calculation of Weighting Factors. The pooled standard error of the mean (SEM) for the variable of interest was included as a weighting factor. In the articles that reported standard error of the difference (SED), the SEM was calculated as follows:

$$SEM = \frac{SED}{\sqrt{2}}.$$

If root mean square error (RMSE) was reported in the study, the SEM was calculated as follows:

$$SEM = \frac{RMSE}{\sqrt{n}},$$

where n is the replications per treatment.

The data were segregated by use of a fixed or mixed model, and SEM were standardized and truncated within fixed and mixed models. To prevent overweighting of studies with extremely low SEM, the SEM was truncated at half of the mean standard error of the mean according to the equation below:

$$SEM_{Trunc} = \text{if : } SEM < \frac{AvgSEM_{Random\ or\ Fixed}}{2}, \\ \text{then } \frac{AvgSEM_{Random\ or\ Fixed}}{2}, \text{ else : } SEM.$$

The weighting factor was calculated with the following formula:

$$Weighting\ factor = \frac{1}{SEM^2}.$$

Last, the weighting factors were standardized to 1 by dividing by the mean within fixed and mixed models allowing use across both model types as follows:

$$Weight_{Standardized} = \frac{Weight}{AvgWeight_{Random\ or\ Fixed}}.$$

Data Analysis. All analyses were performed using JMP Pro 13.0 and 14.0 (SAS Institute). First, descriptive statistics, including distribution and bivariate analysis (mean, median, and SD) were performed to identify outliers and characterize the data set. Next, bivariate regression was performed to determine the correlation with the main variables of interest while modeling the random effect of experiment (random intercept modeled using the default unstructured covariance structure) and using study-weighting as described above. The “full model R^2 ” included the variation accounted for by the random effect of study. The “partial R^2 ,” which is also sometimes called the coefficient of partial determination, represents the R^2 contributed by each fixed effect in the model and was used to determine the correlation with individual predictor. The partial R^2 indicates the proportion of variation explained by each term in the model. Data were also plotted with the Y observation adjusted for the random effect of experiment to best illustrate the biological relationship of interest. Linear and quadratic relationships were tested as diminishing effects were expected for some variables, and the quadratic effect was removed if $P > 0.10$.

Multivariate analysis was then conducted to predict rumination time with or without the random effect of experiment using backward stepwise elimination. The multivariate analysis was first conducted only with the production variables available across most of the studies in the database. This was followed by additional analysis that included dietary NDF concentration and TT DM and NDF digestibility.

Last, principal components analysis was first performed as an exploratory analysis using a selected data set of 7 variables that have been previously related to rumination and milk fat (NDF intake, diet NDF concentration, milk yield, milk fat yield and concentration, DMI, and total rumination time). Principal component analysis was then extended to include a broader set of 39 variables captured in the database [included: TT digestibility of DM, NDF, and starch; milk fat sum of

Table 1. Characterization of diet nutrient composition of treatments included in the meta-analysis

Nutrient ¹	N ²	Mean	Median	Minimum	Maximum	SD
DM, %	308	58.6	57.0	35.4	98.0	10.4
Composition, % of DM						
Forage	72	45.1	45.0	18.4	67.0	11.6
Forage NDF ³	163	20.8	19.6	7.6	67.4	7.34
NDF	337	32.4	32.2	18.2	49.0	4.95
iNDF ⁴	15	11.1	10.5	9.4	15.6	1.73
ADF	261	19.4	19.9	11.3	31.0	3.57
CP	336	17.2	17.1	12.2	22.1	1.51
Starch	182	27.0	26.9	14.5	42.3	5.83
Ether extract	123	3.8	3.5	1.8	6.2	1.19
Fatty acids	43	4.6	4.5	1.5	8.3	1.47
Lignin	51	3.7	3.7	1.1	6.4	1.54

¹Diet composition from the experiments included in the meta-analysis.²Number of treatments reporting the value.³Forage NDF includes forages and beet pulp.⁴iNDF = indigestible NDF. Method of observation varied between experiments.

FA <16 carbons (<C16), *trans*-10,*cis*-12 CLA and *cis* 9,*trans*-11 CLA; ruminal volume and DM and NDF pool size; rumen fluid pH and acetate and total VFA concentration; meal length and size (per kg of DM and NDF) and average intermeal interval; ruminal bout number and length; time spent eating, chewing, and rumination (per d, kg of DMI, and kg of NDF); milk yield, milk fat yield and concentration, protein concentration; diet DM, NDF, NDF from forage, indigestible NDF, ADF, and FA concentration; and peNDF intake].

RESULTS

Characterization of Diets

Diet composition varied drastically among experiments and treatments as expected and averaged 17.2% CP (range: 12.2–22.1%), 20.8% forage NDF (range: 7.6–67.4%), 32.4% NDF (range: 18.2–49.0%), 27.0% starch (range: 14.5–42.3%), and 3.8% ether extract (range: 1.8–6.2%) on a DM basis (Table 1).

Characteristics of Cows, Intake, Milk Production, Rumen pH, and TT Digestibility

The 479 treatment means in the 130 studies represented 1,789 cows with treatment groups ranging from 14 to 292 DIM (Table 2). Milk yield averaged 34.3 kg/d (range: 14.2–52.1), and milk fat averaged 3.47% (range 2.20–4.60). Dry matter intake averaged 23.1 kg/d (range: 15.3–32.6). Mean rumen pH was 6.1 (range: 5.3–7.0) in the 292 treatments reporting the observation. Apparent TT digestibility of DM averaged 67.6% (range: 51.4–78.9), and TT digestibility of NDF averaged 49.3% (range: 23.0–76.0).

The average total time spent ruminating was 444 min/d (range: 151–638). The average of other metrics of rumination time were 19.7 min/kg of DMI (range: 7.6–36.1), 62.9 min/kg of NDF (range: 24.8–127), 13.8 bout/d (range: 7.8–17.4), and average bout length of 32.7 min/d (range: 20.0–48.1).

Characteristics of Rumination Observation Systems and Rumination Behavior

Rumination monitoring by VO averaged 441 min/d (range: 204–638; $n = 253$), and automated systems averaged 447 min/d (range: 151–618; $n = 204$; Table 3). To further characterize the effect of observation method, data were categorized into 6 categories as described above. Total rumination time averaged 392 min/d in Beauchemin 1989 (range: 151–486), 463 min/d in Dado 1993 (range: 310–616), 447 min/d in AJAW systems (range: 242–566), 497 min/d in SCR (range: 357–618), and 412 min/d in the remaining other automated systems (range: 285–503). Observation system was not included in the subsequent regressions as it was accounted for by the random effect of study.

Bivariate Regression of Rumination with Key Variables

Bivariate analysis was conducted to determine the relationship between rumination metrics and key parameters including milk yield, milk fat yield and percent, rumen pH, DM and NDF intake, dietary NDF concentration, and TT NDF digestibility while including the random effect of experiment (Table 4; Figure 1). The correlation with the fixed effect predictor variable was characterized using the partial R^2 to separate variation

Table 2. Description of mean production and rumination metrics of treatments included in the meta-analysis

Item	N ¹	Mean	Median	Minimum	Maximum	SD
Number of cows	479	12.9	9.0	3.0	156	14.9
Intake, ² kg/d						
DM	443	23.1	23.1	15.3	32.6	3.12
Forage	41	9.4	9.6	4.3	17.1	2.65
NDF reported	299	7.3	7.3	4.2	11.3	1.34
NDF calculated	331	7.5	7.6	4.1	10.5	1.39
Starch	65	6.3	6.4	3.1	9.4	1.74
Milk yield, kg/d						
Milk	386	34.3	34.1	14.2	52.1	7.31
Fat	386	1.18	1.17	0.58	1.93	0.26
Milk composition, %						
Fat	386	3.47	3.50	2.20	4.60	0.39
Protein	342	3.16	3.14	2.70	3.80	0.23
Rumen pH	292	6.10	6.10	5.30	7.00	0.29
Rumination						
min/d	458	444	447	151	638	75.20
min/kg of DMI	443	19.7	19.2	7.60	36.1	3.99
min/kg of NDF ³	370	62.9	60.3	24.8	127	15.9
min/kg of forage NDF	69	110	111	51.6	194	30.4
Bouts/d	139	13.8	14.1	7.8	17.4	1.91
Bout length, min	121	32.7	32.7	20.0	48.1	6.1
Total-tract digestibility, %						
DM	141	67.6	67.5	51.4	78.9	5.31
NDF	159	49.3	48.4	23.0	76.0	9.29

¹Number of treatments reporting the variable.²Intake as directly reported in the paper.³NDF intake calculated based on DMI and NDF composition of the diet.

accounted for by the fixed effect from the variation accounted for by the random effect of experiment.

Milk yield was linearly related to the total rumination time per day (min/d; $P < 0.001$ and partial $R^2 = 0.27$; Table 4), with rumination increasing 4.21 min/d with each kilogram increase in milk yield. However, rumination per kilogram of DM and rumination per kilogram of reported and calculated NDF intake was not related to milk yield.

Milk fat yield was quadratically related to total rumination time, rumination per kilogram of DMI, and calculated NDF intake (all $P < 0.01$; partial $R^2 = 0.27$, 0.17, and 0.14, respectively; Table 4), but there was no relationship with rumination per kilogram of reported NDF intake. Milk fat concentration was linearly related to all rumination metrics (all $P \leq 0.02$) except rumination per kilogram of calculated NDF intake ($P = 0.33$). One percentage unit increase in milk fat concentration

Table 3. Description of average rumination time (min/d) reported by different observation methods

System ¹	N ²	Mean	Median	Minimum	Maximum	SD
Visual Obs.	253	441	440	204	638	76
Automated Obs.	204	447	454	151	618	74
Beauchemin 1989	31	392	414	151	486	73
Dado 1993	46	463	474	310	616	62
AJAWS	85	447	463	242	566	73
SCR	28	497	504	357	618	57
Other Auto	14	412	438	285	503	71

¹Visual Obs. = feeding behavior obtained by visual and video recordings observation every 1, 5, or 10 min over 24 or 48 h; Automated Obs. = all automated feeding behavior systems; Beauchemin 1989 = feeding behavior obtained by the automated system described in Beauchemin et al. (1989); Dado 1993 = feeding behavior obtained by the automated system described by Dado and Allen (1993); AJAWS = other automated feeding behavior systems that measured ruminal behavior based on jaw movement including pneumatic systems attached to a cord under the jaw (i.e., Deswysen et al., 1987; Weigand et al., 1993; Beauchemin and Yang, 2005; Zebeli et al., 2007); SCR = feeding behavior obtained by a microphone-based system (SCR Engineers Ltd.); Other Auto = feeding behavior obtained by other sensors that couldn't be grouped with the above categories.

²Number of treatment means in each category.

Table 4. Bivariate analysis of rumination time and milk production, rumen pH, and total-tract digestibility

Variable ¹	Linear			Quadratic			R ²	
	Intercept	Slope	SE	P-value	Slope	SE	Full	Partial
Rumination, min/d	307	4.21	0.72	<0.001	—	—	0.22	0.27
Milk, kg/d	51.9	539	122	<0.001	—	—	0.80	0.27
Milk fat	233	63.3	11.1	<0.001	—	—	0.81	0.17
kg/d	—174	102	15.7	<0.001	—164	49.0	0.85	0.10
%	305	6.12	1.45	<0.001	—	—	0.76	0.21
Rumen pH	72.1	87.4	30.9	<0.01	—	—	0.78	0.19
DMI, kg/d	255	9.58	6.71	0.15	—4.85	2.03	0.02	0.18
NDF intake, kg/d	—40.1	18.5	4.52	<0.001	—0.110	0.102	0.28	0.17
Diet NDF, % of DM	19.5	—0.131	1.09	0.90	—0.177	0.047	<0.001	0.18
TT NDF Dig, ³ %	9.84	16.6	6.83	0.02	—	—	0.73	0.18
Rumination, min/kg of DMI	7.38	3.46	0.567	<0.001	—	—	0.73	0.17
Milk, kg/d	—19.6	6.48	0.86	0.84	—6.84	2.76	0.01	0.17
Milk fat	55.6	—2.45	0.586	<0.001	—	—	0.77	0.17
kg/d	21.3	—0.238	0.206	0.25	—	—	0.88	0.08
%	10.4	0.281	0.049	<0.001	—	—	0.83	0.26
Rumen pH	5.19	0.544	0.249	0.03	0.038	0.013	0.74	0.27
DMI, kg/d	70.1	—0.223	0.244	0.36	—	—	0.79	0.18
NDF intake, kg/d	23.9	63.6	36.4	0.08	—0.005	0.003	0.72	0.23
NDF intake, % of DM	41.8	5.92	2.62	0.02	—	—	0.87	0.08
Diet NDF, % of DM	530	—162	73.7	0.03	—	—	0.87	0.10
TT NDF Dig, %	79.2	—0.787	0.309	0.01	14.0	6.00	0.93	0.04
Rumination, min/kg of NDF (reported NDF intake)	97.3	—4.84	0.818	<0.001	—	—	0.88	0.11
Milk, kg/d	76.3	—0.457	0.227	0.04	—	—	0.88	0.24
Milk fat	74.2	—0.326	0.291	0.11	—	—	0.86	0.15
kg/d	68.0	—0.121	0.184	0.51	—	—	0.91	0.14
%	14.9	87.3	27.4	<0.01	—	—	0.85	0.13
Rumen pH	56.0	2.21	2.24	0.33	—37.1	11.2	<0.01	0.14
DMI, kg/d	—24.1	14.4	3.08	<0.001	—	—	0.86	0.13
NDF intake, kg/d	93.7	—1.34	0.278	<0.001	—	—	0.85	0.07
Diet NDF, % of DM	103	—5.58	0.658	<0.001	—	—	0.85	0.16
TT NDF Dig, %	163	—5.15	1.18	<0.001	—	—	0.84	0.34
Rumination, min/kg of NDF (calculated NDF intake)	7.94	2.26	0.88	0.01	0.060	0.018	0.80	0.31
Milk, kg/d	—	—	—	—	—0.022	0.010	0.87	0.12
Milk fat	—	—	—	—	—	—	—	—
kg/d	—	—	—	—	—	—	—	—
%	—	—	—	—	—	—	—	—
Rumen pH	—	—	—	—	—	—	—	—
DMI, kg/d	—	—	—	—	—	—	—	—
NDF intake, kg/d	—	—	—	—	—	—	—	—
Diet NDF, % of DM	—	—	—	—	—	—	—	—
TT NDF Dig, %	—	—	—	—	—	—	—	—

¹Y = dependent variable in the first heading and X = independent variables in the subheading.²RMSE = root mean square error.³TT NDF Dig = total-tract NDF digestibility.

was associated with a rumination time increase of 63.3 min/d, 3.46 min/kg of DMI, and 5.92 min/kg of reported NDF intake.

Ruminal pH was linearly related to the rumination time per day and per kilogram of calculated NDF intake (both $P < 0.001$; partial $R^2 = 0.10$ and 0.04 ,

Figure 1. Relationship between rumination time and key variables explored with bivariate analysis while accounting for the random effect of experiment. The database was created from 479 treatment means reported in 130 papers. Plotted total rumination time was adjusted (Adj.) for the random effect of experiment. The P -value of the linear (L) and quadratic (Q) effects are shown along with the partial R^2 for the bivariate fit (excludes random effect of experiment). TT NDFd = total-tract NDF digestibility.

respectively; Table 4) and was quadratically related to rumination per kilogram of reported NDF intake ($P = 0.02$). A 0.1-unit increase in rumen pH was associated with a 102 min/d increase in rumination. Rumen pH was not related to rumination per kilogram of DMI.

Dry matter intake was linearly related to rumination time per day and per kilogram of reported and calculated NDF intake (all $P \leq 0.01$; partial $R^2 = 0.21$, 0.11, and 0.16, respectively; Table 4) and quadratically related to rumination per kilogram of DMI ($P < 0.01$; partial $R^2 = 0.26$). Each 1-kg increase in DMI was associated with a 6.12 min/d increase in rumination.

Reported NDF intake was quadratically related to rumination time per day ($P = 0.02$; partial $R^2 = 0.19$; Table 4) and linearly related to rumination per kilogram of reported and calculated NDF intake (both $P < 0.001$; partial $R^2 = 0.24$ and 0.34). A 1-kg increase in NDF intake was associated with a 0.23 min/kg of DMI decrease in rumination.

Dietary NDF concentration was linearly related to rumination per kilogram of DMI and per kilogram of reported NDF intake ($P < 0.001$, $P = 0.04$; partial $R^2 = 0.18$ and 0.15, respectively; Table 4) and quadratically related to rumination per kilogram of calculated NDF intake ($P < 0.001$; partial $R^2 = 0.31$). A 1-unit increase in dietary NDF concentration was associated with an increase in rumination of 0.281 min/kg of DMI. However, dietary NDF concentration was not related to rumination time per day.

Total-tract NDF digestibility was quadratically related to rumination time per day, per kilogram of DMI, and per kilogram of calculated NDF intake ($P < 0.001$, $P = 0.04$, and $P = 0.02$; partial $R^2 = 0.17$, 0.23, and 0.12, respectively; Table 4). One percentage unit increase in TT NDF digestibility was associated with an 18.5 min/d increase in rumination time.

Multivariate Analysis

Multivariate regression was conducted by stepwise removal of nonsignificant terms to predict total rumination time with or without including the random effect of experiment (random intercept modeled using the default unstructured covariance structure; Table 5). Including the random effect provides the best insight into biological mechanisms, whereas the fixed effect model allows characterization of variation expected when applied to future data. Without the random effect of experiment, the final model based on production variables available in all experiments included milk yield and milk fat yield and concentration and had a model R^2 of 0.32. Rumination time increased with milk yield and milk fat concentration, but decreased with increasing milk fat yield. When the random effect of

experiment was included in modeling the production variables, milk fat yield became a quadratic effect and the model partial R^2 of fixed terms increased to 0.37. Multivariate modeling that tested DMI, diet NDF concentration, and TT NDF digestibility, which were only available for a smaller number of observations, did not increase model fit in the fixed effect model, although a negative effect of DMI was retained in the model (Table 5). A quadratic effect of TT NDF digestibility was retained in the random effect model and increased the partial R^2 of fixed terms from 0.37 to 0.41.

Principal Component Analysis

Principal component analysis was used to explore the relationships between variables recorded in the study. The analysis was conducted both in a select set of 7 variables reported in a larger number of studies and with a broader set of 39 variables related to milk fat production.

Using the 7 selected variables, the first principal component (**PC1**) and the second principal component (**PC2**) explained a total of 69.1% of the variation (Figure 2A). Total rumination time, DMI, and milk fat yield were in PC1. The most influential variable in PC1 was milk yield, and the most influential variable in PC2 was diet NDF concentration. Milk fat concentration and dietary NDF concentration were highly correlated, as were total rumination, DMI, milk yield, and milk fat yield.

In the broad analysis, the first 2 principal components, PC1 and PC2, explained only 36.7% of the variation. The factors best explained by the principal components were *trans*-10, *cis*-12 CLA in PC1 and ruminal volume in PC2 (Figure 2B). The variables with the least influence in the first 2 principal components were rumen pH, TT starch digestibility, milk yield, and milk protein concentration. Milk fat yield and concentration were closely related to meal length, diet indigestible NDF, ADF, and NDF from forage, and rumination bout length within PC1 and PC2.

DISCUSSION

It is well recognized that changes in diet composition and management affect rumen function and eating and ruminating behavior. These effects have been investigated extensively in individual experiments over the last 30 yr (e.g., Beauchemin et al., 1989; Dado and Allen, 1994; Ramirez Ramirez et al., 2016; Crossley et al., 2017; Fustini et al., 2017) and discussed in reviews. Allen (1997) conducted a meta-analysis investigating the effect of particle size and diet composition on rumination and chewing time. More recently, White

et al. (2017) summarized the relationship between effective fiber and eating and rumination behavior, and Beauchemin (2018) provided a broad perspective of factors affecting eating and rumination. The current study identified 130 papers with 479 treatment means reporting rumination time with diverse treatments, which allowed for ample power for a meta-regression. These manuscripts reported numerous response parameters, and many interactions could be investigated, but the analysis focused on understanding the relationship between rumination and milk fat production and factors known to affect milk fat. It is important to note that the meta-analysis of White et al. (2017) focused on experiments that investigated physical effective fiber and thus only included less than half the number of papers and treatment means compared with the current study. The average rumination time in the current data set was 21 min longer and slightly larger in range than the physical effective fiber database (236–610 min/d).

Diverse rumination observation methods are used based on the equipment available in individual research laboratories. Individual systems are commonly validated against VO when first developed. For example,

Ambriz-Vilchis et al. (2015) reported a positive correlation between rumination activity measured through rumination collars, video recordings, and VO. The average rumination time among systems was modeled in an exploratory analysis in the current project and was not meant to, nor could it, validate individual systems. Little difference was found among the 6 system groups (Table 3), and differences may be due to types of diets fed in research groups with different systems. Observation system was not included in the subsequent regressions, as the random effect of experiment accounted for differences among systems. Additionally, data were weighted based on standard errors that accounted for differences in precision among systems. Combining data across systems allowed for a robust analysis across the largest range in rumination time and cow, diet, and environmental conditions. It should be noted that not all response variables of interest were reported in all papers. Caution should be taken when comparing among regressions, as the difference in number of papers reporting each observation influences the power of the test. The goal of the study was to investigate the relationship of selected factors with rumination, not to compare among factors.

Table 5. Multivariate prediction of total rumination time¹

Item	Estimate	SEM	P-value	Model	R ²	RMSE	
Model without random effect of experiment							
Only production variables (n = 362)							
Intercept	−282	157	0.07	Full ¹	0.32	79.8	
Milk, kg/d	14.6	4.23	<0.001				
Milk fat, %	158	43.9	<0.001				
Milk fat, kg	−272	119	0.02				
With DMI (n = 358)							
Intercept	−191	162	0.24	Full	0.32	79.6	
Milk, kg/d	14.2	4.24	<0.001				
Milk fat, %	148	44.1	<0.001				
Milk fat, kg	−227	120	0.06				
DMI, kg/d	−4.00	1.74	0.02				
Model with random effect of experiment							
Only production variables (n = 362)							
Intercept	−516	174	<0.01	Full Partial R ² Random Fixed	0.81	46.9	
Milk, kg/d	15.6	5.12	<0.01				
Milk fat, %	185	50	<0.001		0.44 0.37		
Milk fat, kg/d							
Linear	−40.8	219	0.85				
Quadratic	−113	52.2	0.03				
With NDFd (n = 138)							
Intercept	−1963	521	<0.001	Full Partial R ² Random Fixed	0.87	45.8	
Milk, kg/d	38.2	10.1	<0.001				
Milk fat, kg/d	−920	292	<0.01		0.46 0.41		
Milk fat, %							
Linear	738	243	<0.01				
Quadratic	−49.2	28.4	0.09				
TT NDF Dig, ² %							
Linear	8.25	4.37	0.06				
Quadratic	−0.077	0.045	0.09				

¹R² is shown for the full model followed by the partial R² for the random or sum of the fixed terms of the model; RMSE = root mean square error.

²TT NDF Dig = total-tract NDF digestibility.

Figure 2. Principal component analysis of the relationship between variables from 479 treatment means reported in 130 papers observing rumination time. Panel A includes only the 7 main variables hypothesized to be related to rumination and milk fat (NDF intake and diet concentration, milk yield, milk fat yield (MFY) and concentration, DMI, and total rumination time). Panel B includes 39 additional variables collected in the database [total-tract digestibility of DM, NDF and starch; milk fat sum of FA <16 carbons (<C16), *trans*-10, *cis*-12 CLA and *cis*-9, *trans*-11 CLA; ruminal volume and DM and NDF pool size; rumen fluid pH and acetate and total VFA concentration; meal length and size (DM and NDF) and average intermeal interval; ruminal bout number and length; time spent eating, chewing, and rumination (per d, kg of DMI, and kg of NDF); milk yield, milk fat yield and concentration, protein concentration; diet DM, NDF, NDF from forage (NDFr), indigestible NDF (INDF), ADF, and FA concentration, and physically effective (peNDF) intake].

Diet composition varied drastically across experiments, as expected, as they represent very diverse experimental feeding strategies and philosophies; furthermore, some studies tested extreme conditions. This variation also aided the meta-regression by providing a broad range of input and responses variables. Diet composition has been reported to affect ruminal fermentation and function as well as rumination time because rumination is regulated by distension of tension receptors in the rumen, rumen VFA concentration, and osmotic pressure (Beauchemin, 2018). Briefly, increasing diet NDF concentration has been reported to quadratically increase rumination (Beauchemin et al., 1989), decreasing dietary particle size (1.0 mm) decreases time spent ruminating per unit of NDF intake (Grant et al., 1990), and increasing dietary peNDF increases rumination time (Yang and Beauchemin, 2007; White et al., 2017). The relationships between rumination time and diet NDF and NDF intake in the current experiment agreed with these observations; however, independently, these factors only explained a moderate amount of the variation in rumination time (partial $R^2 = 0.18$ and 0.19 , respectively; Table 4 and Figure 1E).

Apparent TT NDF digestibility was quadratically related to rumination time, and maximum digestibility of 52.3% was predicted at 443 min/d of rumination (Table 4; Figure 1F). In the multivariate analysis, TT NDF digestibility was retained in the model, although the partial R^2 was small (0.04). Apparent TT NDF digestibility is a good indicator of DMI, and forages with high NDF digestibility have shorter rumen retention time, which allows for greater DMI (Oba and Allen, 1999). This is because NDF generally ferments and passes from the reticulorumen slower than other dietary constituents (Allen, 1996). Mertens (1994) attempted to predict filling effects and energy content of the diets using diet NDF concentration, and found it was positively correlated with DMI when energy limits intake, but negatively correlated with NDF concentration when fill limits intake. Increased in vitro NDF digestibility is associated with higher energy intake, which results in increased milk yield (Oba and Allen, 1999). Optimal NDF digestion should allow maximal milk fat synthesis, as stable ruminal fermentation would be expected to minimize biohydrogenation-induced milk fat depression and fiber digestion results in acetate synthesis. Ruminal infusion of sodium acetate has been demonstrated to increase milk fat yield (Urrutia and Harvatine, 2017).

Milk yield ($P < 0.001$; $R^2 = 0.27$) and DMI ($P < 0.001$; $R^2 = 0.21$) was not highly correlated with rumination activity (Figure 1A and 1B). Others have also reported low to moderate relationships between rumination time and milk yield, which are expected to be indirect through increased DMI (Beauchemin,

2018). The expected positive relationships between rumination and milk fat concentration and yield were observed, although the relationship was only moderately strong (partial $R^2 = 0.17$ and 0.27 ; Figure 1C and 1D). A positive relationship between rumination and milk fat was hypothesized based on the expectation that increased rumination would increase rumen pH, promoting fiber digestion and normal biohydrogenation pathways and capacity. Milk fat is also decreased during subacute ruminal acidosis and when feeding low forage diets that are also associated with decreased rumination time. For example, in a previous study, Oba and Allen (2003) reported a 15% decrease in milk fat yield when feeding a 32% starch diet that reduced rumination by over 40 min/d. Although the relationship of rumination with milk fat percent was linear in the current meta-regression, the relationship with milk fat yield was quadratic (Figure 1C and 1D, respectively). It is interesting to highlight that there was a stronger relationship in the bivariate fit of rumination and milk fat yield than milk fat percent, although milk fat percent normally has a smaller variance within experiments. The quadratic relationship between rumination and milk fat yield indicated little gain in milk fat yield above approximately 450 min/d. This may be due to energy limitation that reduces potential for milk yield above certain levels of dietary fiber and effective fiber. The best-fit multivariate model for total rumination time included milk yield and milk fat concentration in addition to DMI, further indicating a strong relationship between rumination and milk fat production.

Andreen et al. (2020) recently investigated the relationship between rumination and milk fat concentration over a year in over 1,800 cows on 2 commercial dairies using commercial rumination observation systems. Interestingly, there was a slight negative relationship between rumination time and milk fat percent ($R^2 = 0.009$). Andreen et al. (2021) also investigated the relationship between rumination and milk fat concentration and milk fatty acid profile in 1,733 cows on 5 commercial dairy farms with commercial rumination observation systems. Rumination time was linearly related to *trans*-10 C18:1 in milk fat that was associated with diet-induced milk fat depression, but was not related to milk fat concentration, although the relationship was weak (partial $R^2 < 0.05$). Importantly, these experiments investigated the variation within farm when cows were fed the same diet. Both experiments reported large variation in rumination time among cows that were presumably due to either sensor observation error or nondietary factors. Moreover, the relationships in the current analysis were based on differences across diverse dietary treatments and may not be applicable to differences among cows fed the same diet.

A negative relationship between rumination time per kilogram of NDF intake and DMI (Table 4) may be explained by multiple factors. First, it may be the result of higher DMI when feeding more fermentable and lower NDF diets. Highly fermentable feeds may also have a higher rumen passage rate, reducing rumen fill and rumination time. Last, there is a physiological maximum for total chewing time per day, and increased eating time at higher DMI may limit time available for rumination (Beauchemin, 2018).

Allen (1997) reported a positive relationship between rumen pH and milk fat. Increasing rumen pH may increase fiber digestibility and acetate supply, and increased rumen pH also maintains normal ruminal biohydrogenation (Sun et al., 2019). Although a relationship between rumination and rumen pH was found, it was weak and likely explains only a small part of the milk fat response.

Rumination, rumen pH, and many other factors vary greatly over the day (Salfer et al., 2018). It is important to note that the summation variables of total rumination time per day and average rumen pH fail to account for variation over the course of the day. It is possible that rumination at certain times of the day has a greater influence on rumen environment and milk fat yield. However, rumination is commonly only reported as the total over the day. Future work may identify portions of the day that are more influential and allow development of response variables with greater predictive power.

CONCLUSIONS

Rumination was related to milk yield, milk fat yield and concentration, rumen pH, DMI, NDF intake, and TT digestibility. Milk fat yield was maximal at 494 min/d, with no additional benefit of increased rumination, likely due to negative effect on energy intake above these levels. In multivariate analysis, the set of variables most strongly associated with rumination time were milk yield, milk fat concentration and yield, and DMI. Overall, rumination time was related to milk fat across a large number of studies. However, the relationship was only moderate in overall strength, indicating that rumination is not the only factor important to optimal and stable ruminal fermentation, and factors other than ruminal fermentation affect milk fat production.

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