A QUANTITATIVE ANALYSIS OF RUMINATION PATTERNS

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Summary
Available data concerning rumination have been used to develop a quantitative description of its control. Rumination patterns were examined using cosinor analysis in which least-squares estimates of parameters were made by a derivative-free nonlinear regression technique. The model equation was, \( F = C_0 + C \cos (\omega t + \psi) \), where fraction of time spent ruminating \((F)\) was determined by: \( C_0 \), the level or fitted mean; \( C \), amplitude; \( \omega \), the (fixed) angular frequency fitted; \( t \), time and \( \psi \), phase. For sheep fed either hourly or once daily, \( C \) and \( \psi \) were found to be stable, with the latter corresponding to a mean peak rumination time at 0445 h. In animals fed once daily, \( C_0 \) was higher than those fed hourly. Sheep and goats fed twice daily exhibited two rhythms. The period of each corresponded to a between feeding interval; i.e., 9 or 15 h. Feeding time apparently became the forcing oscillation that entrained the rumination rhythm. The limit to which feeding frequency can be increased before reverting to the 24 h rhythm of animals fed hourly or once daily is not known. A relationship between cell wall component content (CWC) of the diet and \( C_0 \) was found \((r^2 = .657)\) using multiple linear regression in a stepwise manner on data from sheep fed forage diets. Fraction of time spent ruminating, therefore, was estimated for sheep fed hourly by the following equation: \( F = (.040 + .508 \text{ CWC}) - .128 \cos (t + 1.89) \). This same equation can be used for animals fed once or twice daily with suitable adjustments. It is not considered appropriate for sheep fed ground or pelleted forages or high concentrate diets.

(Key Words: Sheep, Rumination, Rhythm, Level, Amplitude, Phase.)

Introduction
Rumination has been considered an important component of digestive function in ruminants for many years. The physical breakdown of resistant material in the rumen is thought to be one of its main functions (Gordon, 1968). Rumination also serves to increase passage from the rumen (Pearce and Moir, 1964) which, in turn, affects feed intake. Many investigators have observed a basic circadian rhythm in rumination [i.e., that more rumination occurs during the early morning hours than at any other time (Gordon and Mc Allister, 1970)]. Physical and chemical composition of the food, feeding frequency (Pearce, 1965), feeding time (Gordon, 1958; Welch et al., 1969), and photoperiod (Ruckebusch and Laplace, 1967; Gordon and Mc Allister, 1970) have all been examined as possible alternants of the underlying rhythm. Little is known, however, about the quantitative nature of factors controlling rumination pattern or their interrelationships. The objective of this study was to analyze available data concerning rumination and formulate a quantitative description of its control.

Materials and Methods
Although there are few biological variables that fail to display 24-h rhythms (Sollberger, 1965), it is considered rare for one to conform to an ideal periodic curve; e.g., a sinusoid (Halberg et al., 1967). Most time plots of rumination data (min/h vs time) from the literature, however, appear to fit this type of curve. The cosinor model of Halberg et al. (1967) was, therefore, chosen to analyze available data. This model uses the equation \( F = C_0 + C \cos (\omega t + \psi) \), where fraction of time spent ruminating \((F)\) is a function of: \( C_0 \), the

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level or fitted mean; C, amplitude; ω, the (fixed) angular frequency; t, time and ψ, phase.

The assumption of an underlying rhythm with a period of 24 h allowed the value of ω to be fixed at unity, provided time was expressed in radians (2π). Least-squares estimates of C0, C and ψ were then made using a derivative-free nonlinear regression technique (Ralston, 1979). Separate estimates of dietary effect on C0 were made using multiple linear regression in a stepwise manner (Douglas, 1979).

A period of little or no rumination has been found to coincide with feeding time in animals fed once daily (Gordon, 1958; Pearce, 1965; Ulyatt et al., 1982; G. C. Waghorn, unpublished data) and twice daily (Pearce, 1965; Gordon and McAllister, 1970; Geoffroy, 1974). This inhibitory effect of feeding on rumination was accommodated by excluding data acquired during feeding from the analyses.

Results and Discussion

Gordon (1958) fed two adult sheep a mixed diet, once daily, while advancing the feeding time by 4 h every 7 d. Jaw movements were recorded, over 4-h intervals, for the last 2 d of each period. His experiments, therefore, resulted in six different estimates of fraction of time spent ruminating at each feeding time. One estimate at each feeding time was excluded as discussed above. Numerical results from the cosinor analysis of his data are given in table 1. They are also compared graphically with observed data in figure 1A.

The data of Pearce (1965) were subjected to the same type of analysis after being converted from number of chews/3-h period to fraction of time spent ruminating. Because it was necessary that the constant used for this conversion be arbitrary, the estimate of C0 was invalid. Estimates of C and ψ were affected only to the extent that number of chews and time spent ruminating differ. In one experiment, a sheep was subjected to six different feeding treatments replicated within a period of 90 d. The treatments of ground oat hay were not included in this analysis. The remaining five treatments included four intakes of a 82% chaffed oat hay-18% chaffed lucerne hay diet and one with roughages and a concentrate. Data for all five treatments were pooled for the analysis because level of feeding only affects C0. Results of the analysis are presented in table 1 and figure 1B.

Four experiments in which chaffed lucerne hay was fed either hourly (from a belt feeder with no refusals) or once daily (in a 0900 to 1200 h meal) to groups of 12 sheep, at dry matter intake levels of 694 and 1,028 g/d, were also analyzed (Ulyatt et al., 1982). Results from examination of these data are shown in table 1 and figures 1C, 1D, 1E and 1F. Analyses of two more data sets in which chaffed lucerne hay (85.6% dry matter, apparent dry matter digestibility 65%) was fed either hourly (772 g dry matter daily) or once daily (758 g dry matter at 0900 h) to three wether lambs averaging 38 kg (G. C. Waghorn, unpublished data) are presented in table 1 and figures 1G and 1H.

### Table 1. Cosinor Analysis of Rumination Data from Hourly and Once Daily Feeding

<table>
<thead>
<tr>
<th>Feeding frequency</th>
<th>Intake level</th>
<th>Level, C0</th>
<th>Amplitude, C</th>
<th>Phase, ψ</th>
<th>Peak time, h: min</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>1X</td>
<td>Low</td>
<td>0.239 ± 0.15</td>
<td>-0.111 ± 0.022</td>
<td>2.12 ± 0.20</td>
<td>0354 ± 45</td>
<td>Pearce (1965)</td>
</tr>
<tr>
<td>1X</td>
<td>Low</td>
<td>0.287 ± 0.025</td>
<td>-0.182 ± 0.032</td>
<td>2.12 ± 0.20</td>
<td>0354 ± 47</td>
<td>Ulyatt et al. (1982)</td>
</tr>
<tr>
<td>24X</td>
<td>Low</td>
<td>0.299 ± 0.019</td>
<td>-0.118 ± 0.027</td>
<td>2.14 ± 0.23</td>
<td>0348 ± 53</td>
<td>Ulyatt et al. (1982)</td>
</tr>
<tr>
<td>1X</td>
<td>High</td>
<td>0.344 ± 0.028</td>
<td>-0.183 ± 0.035</td>
<td>2.05 ± 0.23</td>
<td>0409 ± 53</td>
<td>Ulyatt et al. (1982)</td>
</tr>
<tr>
<td>24X</td>
<td>High</td>
<td>0.320 ± 0.015</td>
<td>-0.061 ± 0.021</td>
<td>1.42 ± 0.35</td>
<td>0635 ± 80</td>
<td>G. C. Waghorn (Unpub. data)</td>
</tr>
<tr>
<td>1X</td>
<td>High</td>
<td>0.362 ± 0.025</td>
<td>-0.195 ± 0.036</td>
<td>1.45 ± 0.18</td>
<td>0627 ± 42</td>
<td>G. C. Waghorn (Unpub. data)</td>
</tr>
</tbody>
</table>

Mean ± est. SE  
-0.128 ± 0.018  1.89 ± 0.10  0447 ± 24

*Estimated value ± its estimated standard error.*
It is apparent from the combined results of these studies as presented in table 1, that rumination rhythms have the same phase ($\omega$) whether feeding occurs hourly or once daily. Amplitude (C) of the rhythm is relatively stable across diets, although within diets, C is larger for animals fed once daily than for those fed hourly. Mean fraction of time spent ruminating ($C_o$) is also greater for animals fed once daily. This observation is readily explained by the already mentioned inhibitory effect of feeding. Data including simultaneous measurements of eating and ruminating behavior in both sheep and goats (Geoffroy, 1974; Ulyatt et al., 1982) support the conclusion that when time spent eating exceeds about 18 min/h, rumination is inhibited. Animals fed hourly spend less than 18 min/h eating whereas those meal fed once daily spend more than 18 min/h eating during the 3 to 4 h meal. An increase in $C_o$ by a factor of 24/21 to 24/20, in the three cases examined, could reflect a desire by the animals to spend the same amount of time ruminating a particular diet whether being fed hourly or once daily. Slight differences in $\psi$ across diets could result from either photoperiod or dietary effects.

A distinctly different pattern is observed in animals fed two equal meals daily. It was reported by Pearce (1965) that, in addition to the nocturnal peak found with once daily feeding, animals fed twice daily exhibit a strong period of rumination in the early afternoon (1200 to 1500 h). Geoffroy (1974) fed five similar diets ad libitum in two meals (0830 and 1730 h) to five sheep and five goats. A graphical analysis of his data also suggested the presence of two distinct cosine patterns. One appeared to have a 9-h period between 0830 and 1730 h; the other a 15-h period between 1730 and 0830 h. Each period, therefore, was examined separately using pooled diet data for each species. The 9-h period was analyzed by changing $\omega$ in the equation to 24/9, whereas for the 15-h period it was changed to 24/15. Results of these analyses are shown in table 2 and figures 2A and 2B for sheep and goats, respectively. Gordon (1958) cautiously concluded that there could still be a relationship between time of feeding and time of ruminating, even though he was not able to affect the rhythm by changing the time of once daily feeding. Our results support the presence of two adjacent rhythms in which the zeitgeber (synchronizer or forcing oscillation which entrains a biological rhythm; Büning, 1973) has become feeding time. The degree to which multiple rhythms can be entrained by increasing feeding frequency is not known; however, animals fed hourly show a free-running period of 24 h. This effect is perhaps analogous to the limited ability of plants and animals to adapt their rhythms to abnormal light-dark cycles (Bünning, 1973). The periodic nature of rumination can be described by C, $\omega$, and $\psi$, whereas $C_o$ is required to set the total rumination time for a particular diet. This time is simply $C_o$ multiplied by the
Figure 2. Least-squares fit of cosinor equations to observed data for fraction of time spent ruminating (proportion of an hour) vs time for animals fed twice daily. Adapted from Geoffroy (1974). A) Sheep; B) Goats.

length of the period to which it applies. Several investigators have reported a relationship between fibrousness of the diet and total time spent ruminating (Hancock, 1953; Welch and Smith, 1969a, 1970; Balch, 1971; Dulphy and Bechet, 1976). More specifically, Welch and Smith (1969a, 1970) found very close correlations between cell wall constituent (CWC) content and rumination time in both sheep and cattle. It has also been commonly observed that animals consuming more of a particular forage diet ruminate longer than those receiving less of the same diet. This effect is nearly linear (Hancock, 1953; Welch and Smith, 1969b; Balch, 1971). An attempt to relate CWC content, dry matter intake (DMI) and their product (CWC intake) to total rumination time was made. Multiple linear regression was applied in a stepwise manner to available data from sheep on forage diets (Weston and Hogan, 1967, 1971; Hogan and Weston, 1969; Hogan et al., 1969; Welch and Smith, 1969a,b; Ulyatt et al., 1982). Independent variables included CWC content (proportion of the feed dry matter), DMI (g/d), and CWC intake (g/d).

Table 2. Cosinor Analysis of Rumination Data From Twice Daily Feeding

<table>
<thead>
<tr>
<th>Species</th>
<th>Time interval, h</th>
<th>Level, ( C_0 )</th>
<th>Amplitude, ( C )</th>
<th>Phase, ( \psi )</th>
<th>Peak time, h ( \pm ) min</th>
</tr>
</thead>
<tbody>
<tr>
<td>Sheep</td>
<td>0830 to 1730</td>
<td>.394 ± .009(^b)</td>
<td>-.198 ± .014</td>
<td>5.84 ± .05</td>
<td>1408 ± 12</td>
</tr>
<tr>
<td></td>
<td>1730 to 0830</td>
<td>.423 ± .026</td>
<td>-.131 ± .039</td>
<td>4.41 ± .27</td>
<td>.0258 ± 62</td>
</tr>
<tr>
<td>Goats</td>
<td>0830 to 1730</td>
<td>.274 ± .032</td>
<td>-.144 ± .051</td>
<td>5.87 ± .26</td>
<td>1405 ± 58</td>
</tr>
<tr>
<td></td>
<td>1730 to 0830</td>
<td>.381 ± .030</td>
<td>-.290 ± .044</td>
<td>4.38 ± .14</td>
<td>.0303 ± 31</td>
</tr>
</tbody>
</table>

\(^a\)Geoffroy (1974).

\(^b\)Estimated value ± its estimated standard error.
Rumination time (min/d) was the dependent variable. A large range of CWC and DMI were represented, from 35.5 to 75.6% and 609 to 1,313 g, respectively. The only variable that entered the equation was CWC ($p < .001$). Apparently not enough data were available in which the same diet was fed at various intakes to justify including DMI in the equation. The equation describing effect of CWC on total rumination time ($Y$) was: $Y = 57.95 + 732.23 \text{CWC}$. This equation is graphed with the observed data in figure 3; its coefficient of determination was .657. For hourly fed animals, the relationship can be translated into the following equation: $C_O = .040 + .508 \text{CWC}$. When combined with the mean $C$ and $\psi$ from table 1, another equation for estimating fraction of time spent ruminating is obtained: $F = (.040 + .508 \text{CWC}) - .128 \cos (t + 1.89)$. The functional form of this equation can be used for once or twice daily feeding provided $\alpha$ is adjusted as outlined above.

While diets including ground or pelleted forages or concentrate have not been considered, the equations developed provide a quantitative description of both the magnitude and pattern of rumination.

**Literature Cited**


