QUANTITATIVE ANALYSIS OF NYCTEROHEMERAL EATING AND RUMINATING PATTERNS IN HEIFERS WITH DIFFERENT VOLUNTARY INTAKES AND EFFECTS OF MONENSIN

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ABSTRACT

The nycterohemeral pattern of eating and ruminating behavior was examined in six heifers given ad libitum access to a corn silage-based diet with or without 100 mg monensin·hd⁻¹·d⁻¹ in a two-period crossover design. Rhythm components (no. of cycles/24 h) were characterized by the finite Fourier transform of 24-h mastication activities series measured over 7 d. Analysis of variance of the daily mean of hourly activities and rhythm components 1 to 12 showed significant effects of heifer (H), monensin treatment (T), period (P) and T x P x H interactions. A reparameterization of the finite Fourier transform yielded the amplitude and the phase for each rhythm component and allowed the plot of periodograms and phase diagrams, respectively. Rhythm components 1, 2 and 3 contributed primarily in explaining the total dispersion of 24-h eating and ruminating mastication series. The major effect of monensin was to increase the phase at rhythm component 1, delaying by 1 h the onset of rumination after the morning feeding. Heifer effects were significant and appeared related to variations in daily voluntary intake (VI) of individual heifers. Heifer 5, with the largest VI, had two main eating periods and the highest rate of eating. Heifer 4, with the smallest VI, partitioned mastication activity throughout the day into four main eating and ruminating periods. Differences among animals in their nycterohemeral chewing behavior patterns may be related to differences in forestomach structure associated with a larger VI capacity by animals having mastication rhythm components 1 and 3.

(Key Words: Voluntary Intake, Mastication, Rumination, Diurnal Variation, Monensin.)


Introduction

Eating and ruminating activities are important components of digestive function in ruminants. The major reason for studying the feeding and ruminating patterns of animals is to understand both the behavioral and physiological processes that control feeding (Pank-
complex rhythmic patterns of hourly eating and ruminating mastication activities and to relate such patterns to effects of monensin treatment and to variations in voluntary intake among individual cattle.

**Materials and Methods**

**Animals and Measurements.** Six 18-mo-old, 1/4 Brahman × 1/4 Jersey × 1/2 Angus heifers (290 kg average BW) had ad libitum access to corn silage with or without added monensin (100 mg-heifer⁻¹-d⁻¹) in two daily meals at about 0900 and 1800, according to a two-period crossover design (Cochran and Cox, 1957). The daily amounts offered to individuals were 115% of that consumed during the previous day. A supplement of 454 g of cottonseed meal with or without 100 mg monensin and 100 g of trace mineralized salt was provided at 1800 and eaten within a few minutes. The corn silage and cottonseed meal contained, respectively, 32.5 and 90.5% DM; DM contained 8.0 and 46.8% CP and 50.5 and 31.8% NDF. Daily voluntary intake of corn silage was measured during the last 22 d of each 43-d experimental period. Throughout the experiment (March through May) heifers were kept under 24-h artificial lighting.

Eating and ruminating behavior was recorded continuously for the last 7 d. Chewing movements were sensed by a sponge-filled rubber balloon fitted under the heifer’s lower jaw. The resulting pressure changes were recorded on a multichannel recorder and evaluated as described by Deswysen et al. (1987b). Eating and ruminating mastication times (min) and the number of rumination bolus continuously observed in the measurement period were expressed as hourly and daily mean values. The mean duration (min) of consecutive rumination bolus cycles (Deswysen et al., 1987b) was calculated as hourly and daily values.

**Mathematical Background and Statistical Models.** The current data represent a time series of 24 hourly observations on behavior attributes \{y_t; t = 1, . . . ,24\} where \( y_t \) represents the value at hour t. If \( Y_\omega \) represents its finite Fourier transform at frequency \( \omega \), the following definition is given for \( 0 \leq \omega \leq \pi \):

\[
Y_\omega = \sum_{t=1}^{24} y_t e^{i\omega t} / \sqrt{2\pi} \cdot 24
\]

where \( e^{i\omega t} = \cos(\omega t) + i \sin(\omega t) \), known as Euler’s identity.

Angular frequencies, \( \omega \), are expressed in terms of radians per hour. They may be converted into frequencies expressed in terms of number of cycles over the 24-h period as follows: frequency (no. of cycles/24 h) = \((24/2 \pi) \times \) angular frequency (radians/h).

The Fourier series development of the 24-h behavior series \( \{y_t; t = 1, . . . ,24\} \) is given by:

\[
y_t = a_0 + \sum_{p=1}^{12} \left[ a_p \cos(\omega_p t) + b_p \sin(\omega_p t) \right]
\]

where

\( \omega_p = \frac{2\pi p}{24}, \quad (p = 1, . . . ,12), \) represents the angular frequency corresponding to p cycles over the 24-h period;

\( a_0 = \frac{1}{24} \sum_{t=1}^{24} y_t \), the daily mean of hourly activities; and

\( a_p = \frac{1}{12} \sum_{t=1}^{24} y_t \cos(\omega_p t) \) and \( b_p = \frac{1}{12} \sum_{t=1}^{24} y_t \sin(\omega_p t), (p = 1, . . . ,11), \)

\( a_{12} = \frac{1}{24} \sum_{t=1}^{24} y_t \cos(\pi t) \) and \( b_{12} = 0 \), represent, up to a multiplicative constant, respectively, the real and imaginary parts of the finite Fourier transform at the corresponding frequency.

\(^4\)Contained (in % of DM): NaCl, 93; Zn, .035; Mg, .028; Fe, .018; Cu, .035; I, .007 and Co, .007.
A biological interpretation in terms of real and imaginary parts of the finite Fourier transform is not easy. The use of amplitude and phase for frequency components of behavior series may be more appropriate (Deswysen et al., 1986). This is possible by the following reparameterization of (1):

\[ y_t = a_0 + \sum_{p=1}^{12} A_p \cos(\omega_p t + \phi_p) \]  

(2)

where

\[ A_p = \sqrt{a_p^2 + b_p^2} \]  
\[ \phi_p = \arctg \left(\frac{-b_p}{a_p}\right) \]  

(p = 1, ..., 12), respectively, represent the amplitude and the phase at frequency \( \omega_p \) corresponding to \( p \) cycles over the 24-h period, with \( \phi_{12} = 0 \) and \( \arctg \), the arctangent function.

Squared amplitudes \( A_p^2 \) (p = 1, ..., 12), represent, up to a multiplicative constant \((4\pi/12)\) for \( p = 1, \ldots, 11 \) and \( \pi/12 \) for \( p = 12 \), the squared modulus of the finite Fourier transform \( Y_{\omega_p} \), which is called the periodogram. The sum of the ordinates of the periodogram at frequencies \( \omega_p \) (p = 1, ..., 12) is equal to the total dispersion of the 24-h behavior series (Priestley, 1981).

Angular phases \( \phi_p^2 \) (p = 1, ..., 12) are expressed in terms of radians. They may be converted into terms of number of hours as follows: phase (no. of hours) = \([24/(2\pi \cdot p)] \times \) angular phase (radians).

An initial linear model was considered for the hourly behavior attributes measured 7 d in a two-period crossover design. A second linear model was the basis for analysis in the frequency domain and was obtained from the former after finite Fourier transform application. Brillinger (1973) originally introduced this procedure for the study of time series collected in experimental designs.

Data (2,016 individual hourly observations: 6 heifers \( \times \) 2 treatments \( \times \) 24 h \( \times \) 7 d) were collected according to a two-period crossover design (Cochran and Cox, 1957). An hourly time effect and its interactions with terms usually present in a crossover model were added in order to account for within-day variations in behavior. All factors are considered as fixed, even the individual animal, so that the conclusions are specified for the individual heifers of this experiment. Considering experimental days within periods as replicates, the initial linear model (3) for the 24-h behavior series is:

\[ y_{ijkl} = \mu + \delta_i + \lambda_j + \theta_k + (\delta\lambda\theta)_{ijk} + \gamma_t + (\delta\gamma)_{jt} + (\theta\gamma)_{kt} + (\delta\lambda\theta\gamma)_{ijkl} + e_{ijkl} \]  

(3)

where:

\[ y_{ijkl} = \text{behavior measurement for individual heifer } i, \text{ treatment } j, \text{ period } k, \text{ hour } t \text{ and day } l; \]
\[ \mu = \text{mean intercept}; \]
\[ \delta_i = \text{effect of individual heifer, 5 df}; \]
\[ \lambda_j = \text{effect of treatment (with or without monensin), 1 df}; \]
\[ \theta_k = \text{effect of period, 1 df}; \]
\[ (\delta\lambda\theta)_{ijk} = \text{individual heifer } \times \text{ treatment } \times \text{ period interaction, 4 df (incomplete)}; \]
\[ \gamma_t = \text{effect of hour of day, 23 df}; \]
\[ (\delta\gamma)_{jt} = \text{individual heifer } \times \text{ hour of day interaction, 115 df}; \]
\[ (\lambda\gamma)_{jt} = \text{treatment } \times \text{ hour of day interaction, 23 df}; \]
\[ (\theta\gamma)_{kt} = \text{period } \times \text{ hour of day interaction, 23 df}; \]
\[ (\delta\lambda\theta\gamma)_{ijkl} = \text{individual heifer } \times \text{ treatment } \times \text{ period } \times \text{ hour of day interaction, 92 df (incomplete)}; \]
\[ e_{ijkl} = \text{random error, 1,728 df}. \]

Because observations were hourly measurements repeated on the same individuals, the classical variance analysis hypothesis of independence is not satisfied. Exact F-tests are not allowed without a supplementary hypothesis.

Within-day variations in specific behavior and treatment effects are represented in (3) by individual heifer \( \times \) hour of day interaction, \( (\delta\gamma)_{jt} \), and treatment \( \times \) hour of day interaction, \( (\lambda\gamma)_{jt} \). However, these interactions, if signifi-
cant, yield only fragmentary information. Differences among individual animals or treatments in within-day variations must be studied frequency by frequency in order to be of real interest. By providing a spectral decomposition, finite Fourier transform allows analysis in the frequency domain. Its statistical properties of normality and independence have been established by Brillinger (1975, 1983).

Finite Fourier transform at frequency $\omega_p = (2\pi p)/24$, $(p = 1, \ldots, 11)$, of a behavior series $\{Y_t; t = 1, \ldots, 24\}$ correspond, in a general linear model and variance analysis context, to application of a contrasts matrix:

$$C_p = 1/\sqrt{2\pi \cdot 24} \begin{pmatrix} \cos (\omega_p) & \cos (2 \omega_p) & \ldots & \cos (24 \omega_p) \\ \sin (\omega_p) & \sin (2 \omega_p) & \ldots & \sin (24 \omega_p) \end{pmatrix}$$

where $\sum_{t=1}^{24} \cos(\omega_p t) = \sum_{t=1}^{24} \sin(\omega_p t) = 0$.

When the behavior series is arranged into a 24-component vector $y = (y_1 \ldots y_t \ldots y_{24})$, the finite Fourier transform $Y_{\omega_p}$, $(p = 1, \ldots, 11)$ may be written in matrix notation as a two-component vector (real and imaginary parts):

$$Y_{\omega_p} = \begin{pmatrix} \sum_{t=1}^{24} y_t \cos (\omega_p t) / \sqrt{2\pi \cdot 24} \\ \sum_{t=1}^{24} y_t \sin (\omega_p t) / \sqrt{2\pi \cdot 24} \end{pmatrix} = C_p y$$

For frequency $\omega_{12} = (2\pi \cdot 12)/24 = \pi$, $C_{12} = 1/\sqrt{2\pi \cdot 24}$ (-1 1 -1 ... -1 1) is a contrast. For frequency $\omega_0 = (2\pi \cdot 0)/24$, 0 corresponds to an infinite period and $C_0 = 1/\sqrt{2\pi \cdot 24}$ (1 1 1 1 ... 1 1) no longer constitutes a contrast, but the linear transformation based on $C_0$ concerns the mean of the 24 hourly within-day observations.

The finite Fourier transform of (3) at $\omega_p$, $(p = 0, 1, \ldots, 12)$, with vanishing of all terms not depending on hour of day $t$ in (3) and omission of $\omega_p$ subscript (which no longer corresponds to a classification factor), gives an analysis in the frequency domain of a linear (bivariate for $p = 1, \ldots, 11$ and univariate for $p = 0, 12$) model (4) similar to a crossover analysis:

$$Y_{ijkl} = \Gamma + \Delta_i + \Lambda_j + \Theta_k + (\Delta \Lambda \Theta)_{ijk} + E_{ijkl}$$

where:

$Y_{ijkl}$, $\Gamma$, $\Delta_i$, $\Lambda_j$, $\Theta_k$, $(\Delta \Lambda \Theta)_{ijk}$ and $E_{ijkl}$ represent, respectively, finite Fourier transform of $\{Y_{ijkl}; \gamma_t, (\delta \gamma)_t, (\lambda \gamma)_t, (\theta \gamma)_t, (\delta \lambda \gamma)_t, e_{ijkl}; t=1, \ldots, 24\}$;

$\Gamma$ = mean intercept;
$\Delta_i$ = individual heifer effect, 5 df;
$\Lambda_j$ = the monensin treatment effect, 1 df;
$\Theta_k$ = period effect, 1 df;
$(\Delta \Lambda \Theta)_{ijk}$ = individual heifer $\times$ treatment $\times$ period interaction, 4 df (incomplete);
$E_{ijkl}$ = random error, 72 df.

For each frequency $\omega_p$, $(p = 0, 1, \ldots, 12)$, individual heifer, treatment and period effects, and their interaction in (4), were tested classically (e.g., against the residual).

Mean daily voluntary DM intake, eating and ruminating mastication activities data were subjected to ANOVA for a two-period crossover design (Cochran and Cox, 1957). The 11 df for the daily means were partitioned by this
model into monensin treatment, 1 df; period, 1 df; individual heifers, 5 df; and residual or error, 4 df. Individual animals were considered as fixed and were compared using Duncan's multiple range test (Miller, 1981) when a significant heifer effect was detected.

**Results and Discussion**

**Voluntary Intake, Eating and Ruminating Activity.** Daily means for voluntary intake of corn silage DM and eating and ruminating mastication activities of each heifer fed corn silage with and without monensin are summarized in Table 1. There were significant differences among animals in 1) voluntary intake, 2) daily and unitary eating and ruminating times and 3) duration of a meal and of consecutive rumination bolus cycles. Larger voluntary intakes were associated primarily with smaller unitary times (min/[g DM\(^{-1}\)·(kg BW\(^{0.75}\))\(^{-1}\]) for eating and ruminating mastication activities as earlier discussed by Deswysen et al. (1987a). The daily means for eating and ruminating times, the duration of consecutive rumination bolus cycles and the duration of a meal varied among individual heifers. However, variations in the daily mean for these attributes were not clearly associated with voluntary intake. Alternatively, the distribution of eating and ruminating activities could be different within the 24 h and thereby be associated with different voluntary intake levels. Therefore, dominant rhythm components were investigated for mastication activities of eating, ruminating and duration of consecutive rumination bolus cycles, when expressed as hourly values.

**Spectral Analysis.** Results of the analysis of variance of the daily mean of hourly activities and of rhythm components 1 to 12 are summarized in Tables 2 through 4. Rhythm components correspond to the integer number of cycles occurring over 24 h.

The effect of the monensin treatment (T) on the proportion of time spent via ruminating mastication was significant (P = .013) only with rhythm component 1 (Table 3). In contrast, there was no significant effect of monensin on the daily mean of hourly time proportions spent via ruminating mastication (0 cycle/24 h, P = .318, Table 3).

The effect of monensin on hourly mean duration of consecutive rumination bolus cycles was significant for rhythm components 7, 8 and 11 (P = .005, .001 and .036; Table 4). There was no significant effect of monensin on
the daily mean duration of consecutive rumin- 

tation bolus cycles (0 cycle/24 h, \( P = .681 \); 

Table 4).

Significant differences (\( P < .05 \)) among 

individual heifers occurred for nycterohemeral 

rhythm in time proportions for both eating 

(Table 2) and ruminating (Table 3) mastication 

rhythm components 1, 2, 3, 4 and 6 and for 

daily mean of hourly time proportions (0 

cycle/24 h). Significant differences (\( P < .05 \)) 

among individual heifers in the nycterohemeral 

rhythm of hourly mean duration of consecutive 

rumination bolus cycles occurred for all 

rhythm components except 1 and 7 (Table 4).

Effects of period and treatment \( \times \) period \( \times \) 

heifer interactions were significant (\( P < .05 \)) at 

several rhythm components for both eating and 

ruminating mastication time proportions and 

for hourly mean duration of consecutive 

rumination bolus cycles.

Relative Contribution of Rhythm Compo-

nents. Finite Fourier transform of a behavior 

series were reparameterized for each rhythm 

component into its amplitude and phase. 

Because all individual heifers were fed at the 

same hour of the day, the phase should be of 

small importance. The amplitude, however, is 

of biological interest and may vary with 

treatment and individual heifer. The contribu-

tion of a rhythm component to the total 

dispersion of a 24-h mastication series is 

represented by the magnitude of its squared 

amplitude, that is, a periodogram (Priestley, 

1981). Periodograms of eating and ruminating

TABLE 2. ANALYSIS OF VARIANCE OF MEAN 24-HOUR TIME PROPORTIONS 

SPENT EATING MASTICATION (MIN/H) AND OF THE FINITE 

FOURIER TRANSFORM FOR EACH RHYTHM COMPONENT

<table>
<thead>
<tr>
<th>Number of cycles per 24 h</th>
<th>Treatment (T)</th>
<th>Period (P)</th>
<th>Heifer (H)</th>
<th>( T \times P \times H )</th>
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</thead>
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<td>.001</td>
<td>.075</td>
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<td>.005</td>
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<td>.075</td>
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<td>.573</td>
<td>.752</td>
<td>.436</td>
<td>.025</td>
</tr>
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</table>

*Analysis of daily mean of hourly time proportions.
mastication rates and hourly mean duration of consecutive rumination bolus cycles for the six individual heifers are plotted in Figures 1, 4 and 6. A minimal threshold of importance is given by the 10% value of the total dispersion of 24-h mastication series calculated for the individual or treatment mean and indicated in Figures 1, 4, 8 and 9. Hourly means of behavior attributes were calculated on the basis of hourly observations for each heifer (2 treatments x 7 d) and each treatment (6 heifers x 7 d) and used for plots of periodograms and phase diagrams.

**Eating Mastication.** The pattern of time proportions of eating mastication was mostly described by rhythm components 1, 2 and 3 (Figure 1). Rhythm components 1 and 3, and to a lesser extent 2, contributed substantially to the total dispersion of time proportion involving the 24-h eating mastication series of all six individual heifers. Additionally, rhythm components 4 and 5 for heifer 6 and rhythm components 5 and 6 for heifer 4 contributed 12 to 17%, respectively, of the total dispersion for the 24-h eating activity series. The phases of eating mastication time proportion series were largest at rhythm components 1, 2 and 3, with a 1.6-h maximal difference between heifers at rhythm component 1 (Figure 2).

In a previous trial, dominant periodicity of 24 h (rhythm component 1) was observed for the voluntary intake of a complete pelleted diet in 15 of 18 bulls (Stroup et al., 1987). Rhythm component 1 for eating behavior also was observed in cattle fed hay ad libitum once daily (Jaster and Murphy, 1983) and for sheep and cattle fed ad libitum grass silage twice daily (Deswyssen et al., 1986).

A further comparison of periodograms suggests that the patterns of variation in eating mastication activities may be quite different for each animal. This is evident from comparing periodograms for heifers 4 and 5, which had the smallest and largest daily VI, respectively (Table 1). Compared with heifer 5, the eating mastication time proportion of heifer 4 (with the smallest VI) had relatively larger amplitudes for rhythm components 1, 5 and 6 and smaller amplitudes for rhythm components 2 and 3 (Figure 1). Both heifers exhibited a similar phase at these rhythm components (Figure 2). Thus, heifer 4 partitioned the time proportion involving eating mastication throughout the 24 h into four main meals.

**Figure 3.** Nycterohemeral patterns for proportions of time spent eating mastication (---) and ruminating mastication (----) for heifers 4 and 5. Note inverse relations between time proportions for eating and ruminating mastication and nocturnal effects.

**Figure 4.** Periodogram plot of proportions of time spent ruminating mastication (min/h)² of heifers 1 to 6. Note dominant contribution of rhythm components 1, 2 and 3 to the total daily dispersion and differences between heifers 4 and 5.

**Figure 5.** Phase diagram of proportions of time spent ruminating mastication (min/h) of heifers 1 to 6. Note largest phases at rhythm components 1, 2 and 4, and apparent large phase differences among heifers at rhythm components 4, 7, 8, 9, 10 and 11.
TABLE 3. ANALYSIS OF VARIANCE OF MEAN 24-HOUR TIME PROPORTIONS SPENT RUMINATING MASTICATION (MIN/H) AND OF THE FINITE FOURIER TRANSFORM FOR EACH RHYTHM COMPONENT

<table>
<thead>
<tr>
<th>Number of cycles per 24 h</th>
<th>Treatment (T)</th>
<th>Period (P)</th>
<th>Heifer (H)</th>
<th>T x P x H</th>
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</table>

aAnalysis of daily mean of hourly time proportions.

unequally spaced in time, as indicated in Figure 3. In contrast, heifer 5 (with the largest VI) exhibited dominant rhythm components 1 and 3 corresponding to two main meals following the twice daily feeding of fresh silage (Figure 3).

The time proportions for eating mastication of heifer 4, with more main meals and shorter dominant rhythm components, resembles that expected of intermediate to concentrate selectors. Concentrate selectors apportion meals throughout the day with intervening rumination periods (Hofmann and Schnorr, 1982). The two main eating periods of heifer 5 are typical of the meal pattern of roughage eaters. Compared with concentrate selectors, roughage eaters are anatomically characterized by a larger reticuloruminal capacity, which allows larger individual meals and a higher daily VI (Hofmann and Schnorr, 1982). Compared with roughage eaters, the selectivity of intermediate to concentrate selectors presumably results in a lower rate of eating. A larger (P < .05) unitary eating time (min/[g DM^{-1}-(kg BW^{-75})^{-1}]) and thus a slower rate of eating, was observed in heifer 4 than in heifer 5 (Table 1). This clearly suggests that heifer 4, with the smallest VI, behaved more like an intermediate to concentrate selector and heifer 5, with the largest VI, behaved typically as a roughage eater.

Rumination. As for eating mastication time proportions, rhythm components 1, 2 and 3 contributed substantially to the total dispersion of the 24-h proportion of time spent ruminating mastication for the six individual heifers. Additionally, rhythm components 5 and 6 for heifer 4 contributed, respectively, 13.7 and 17.1% to the total daily dispersion of 24-h ruminating activity series (Figure 4). The phases of time proportion spent ruminating mastication were largest at rhythm components 1 and 2, with a 2.0-h maximal difference between heifers 1 and 2 at rhythm component 1 (Figure 5). The apparent large phase differences among heifers at rhythm components 4, 7, 8, 9, 10 and 11 are, in fact, only of small importance For example, the phase for heifers 1, 4, 5 and 6 averaged 5.5 h for rhythm component 4, compared with 0 for heifers 2 and 3 (Figure 5). This difference among heifers (5.5 h) is only .5 h less than the 6-h interval for four cycles/24 h.

Eating and ruminating activities are competitive for the allocation of mastication time and start at feeding, with an increasing or decreasing pattern, respectively (Figure 3). The mean of phase for all heifers at rhythm component 1 is, respectively, 16.7 h and 4.8 h for eating (Figure 2) and rumination activities (Figure 5). Thus, eating and ruminating mastication activities are alternate activities that are spaced in their phase at rhythm component 1 by 11.9 h (16.7 h for eating minus 4.8 h for rumination). It is suggested that the rhythm component 1 for ruminating mastication time proportion results from more consistent ruminating during the early morning hours than at any other time. This basic circadian rhythm component (Gordon, 1958; Gordon and McAllister, 1970; Bae et al., 1979) is quantitatively described by a sinusoidal function (Murphy et al., 1983).
Rhythm component 3 observed here (Figure 4) appears to be caused primarily by the twice-daily feeding at around 8 h daylight interval (0900 and 1800) together with a nocturnal peak. Other observations in sheep (Pearce, 1965), goats (Geoffroy, 1974) and cattle (Deswysen et al., 1986) indicate that animals fed twice daily exhibit a strong period of rumination in the early afternoon in addition to the nocturnal peak. Rhythm component 2 for the nycterohemeral rumination activity (Figure 4) contributed much more to the total 24-h rumination dispersion than did eating mastication associated with the time proportion (Figure 1). This reflects a stronger diurnal and nocturnal periodicity for rumination than for eating mastication, as has been earlier demonstrated for these same data (Deswysen et al., 1989). In cattle with ad libitum access to grass silage twice daily, the time proportion spent via ruminating mastication was described by rhythm components 1 and 3 (Deswysen et al., 1986).

A comparison of periodograms among individual heifers indicates that the magnitude of the periodogram’s ordinates also were more variable among heifers (especially for rhythm component 2) for the time proportion spent as ruminating mastication than for eating mastication. A similar observation was made for the phase diagrams, especially at rhythm component 1. The allocation of time between eating
Figure 8. Periodogram plot of proportions of time spent ruminating mastication (min/h) for heifers receiving the control (C) and monensin (M) treatment. Note dominant contribution of rhythm components 1, 2 and 3 to the total daily dispersion and small reductions in amplitude due to monensin at these rhythm components.

Figure 9. Periodogram plot of hourly mean duration of consecutive rumination bolus cycles (min) for heifers receiving the control (C) and monensin (M) treatments. Note the effect of monensin in increasing the contribution of rhythm components 1 and 2.

and ruminating activities thus appears to be individual-dependent.

Rumination Bolus Cycle Duration. Periodogram analysis of hourly mean duration of consecutive rumination bolus cycles revealed a complex combination of several rhythm components with a dominance of rhythm components 1, 2 and, to a lesser extent, 3 (Figure 6). Rhythm component 1 corresponds to the presence of consistently shorter rumination boli cycles during the day than during the night (Figure 7), as has been earlier demonstrated for these same data (Deswysen et al., 1989). This pattern also has been observed in sheep and cattle fed long grass silage and, in that case, was due to the presence of a strong ruminal interwoven raft that delayed escape of ingestively masticated particles into the reticulum (Deswysen and Ehrlein, 1981). Rhythm component 3 apparently is caused primarily by the twice-daily feeding at around 8 h daylight interval (0900 and 1800). This feeding interval, together with the progressive increase in escape of particles from the ruminal raft during intervening rumination, could allow time for a gradual increase in rumination bolus cycle duration (Figure 7). As for the proportion of time spent ruminating mastication, rhythm component 2 for hourly duration of consecutive rumination bolus cycles should reflect a diurnal and nocturnal periodicity.

Monensin Effect. The variance analysis of finite Fourier transform indicated a significant effect of monensin solely on the 24-h ruminating mastication time proportion for rhythm component 1 (Table 3) and on hourly mean duration of consecutive rumination bolus cycles for rhythm components 7, 8 and 11 (Table 4). However, periodograms of these two ruminating activities (Figures 8 and 9) indicate only small differences between treatments for these significant rhythm components.

The significant effect of monensin on proportion of time spent via ruminating mastication at rhythm component 1 appears mostly due to effects of monensin on the phase (Figure 10). Relative to the control, monensin delayed the onset of ruminating mastication following the morning feeding by approximately 1 h for rhythm component 1. A similar 1-h delaying effect of monensin on the hourly mean duration of consecutive rumination bolus cycles was found at rhythm components 7, 8 and 11. The delaying of rumination activity is in agreement with a trend for longer morning
main meal and daily mean latency time for the onset of rumination due to monensin as reported earlier for these same animals (Deswysen et al., 1987b). The apparent large phase differences between treatments, respectively, of 3.1 h and 2.0 h at rhythm components 7 and 9 (Figure 10) are in fact small. These differences between phases are only .3 h and .7 h less than the 3.4-h and 2.7-h intervals, respectively, for 7 and 9 cycles/24 h.

In conclusion, periodogram analysis of 24-h behavior activities series showed strong rhythmic patterns with rhythm components 1, 2 and 3 contributing mostly to the total dispersion. The nycterohemeral eating and ruminating mastication activities in heifer 5, with the largest voluntary intake, were primarily characterized by rhythm components 1 and 3 and a faster eating rate (fewer minutes of mastication per unit dry matter consumed), such as occurs in roughage eaters. The nycterohemeral rhythm components of these activities in heifer 4, with the smallest VI, were characterized by four major rhythm components and a lower rate of eating, characteristics suggestive of intermediate to concentrate selectors, as shown by Hofmann and Schnorr (1982).

Differences among animals in the nycterohemeral behavior pattern demonstrated by spectral analysis may be related to differences in anatomical size and structure of the forestomach of animals with dominant mastication rhythm components 1 and 3, which are associated with faster rates of eating and a larger VI capacity.

**Literature Cited**


