

Advanced Methods for Evaluating Characteristic Parameters (τ , α , ρ) of Circadian Rhythms*

G. J. Dörrscheidt and L. Beck, Bochum

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Summary

The methods proposed consist of an extension of the classical periodogram method for period evaluation, and of a new approach giving better estimates of activity time α . The improvements of the periodogram method aim at eliminating possible misinterpretations by introducing a confidence limit for "true" periods and by an analysis of homogeneity. Further, the extended method enables one to evaluate τ even from records containing gaps, e.g. caused by feeding intervals. The application of the methods is demonstrated using records of the locomotor activity of the scorpion-spider *Admetus pumilio*.

1. Introduction

The basic parameter of a periodic phenomenon is its period τ (or its inverse, frequency). For the description of the extent of locomotor activity (the most frequently studied periodic animal phenomenon) activity time α , or its complement, rest time ϱ , turned out to be very useful as additional parameters. Usually, τ , α and ϱ are evaluated in a common operation. When the activity record is given in an amplitude-coded form, for instance as a series of hourly activity counts, then the outset and the end of activity time are generally defined by some auxiliary specifications, e.g. by introducing a threshold of 5% of the maximum activity within a certain interval.

However, activity is often recorded by an event recorder as a series of uniform marks. In this case the record is cut into 24-hour sections which are then arranged one below another to yield an "Actogram" representation of the data. The best boundary lines between "activity" and "rest" are estimated by eye from this diagram. Finally, τ and α are drawn as slope of and distance between the boundary lines respectively (Aschoff and Wever 1962).

These methods are rather unreliable and, as is evident from the literature, unsatisfactory. For instance, Aschoff and Wever (1962) required that 3 persons

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have to fix the boundary lines independently. Lohmann (1967) stated that "often it is not possible to determine onset and end of activity unequivocally". In investigating locomotor activity of the scorpion-spider *Admetus pumilio* Beck (1972) found that these difficulties increase further if the pattern of the activity changes, for example from one burst of activity to several bursts in each period. Under conditions of continuous illumination (LL) at low intensities ($< 10^{-3}$ lux) activity records of *Admetus* showed wide fluctuations of magnitude and duration so that τ could be chosen almost arbitrarily. Activity often petered out very slowly making it highly problematic to separate activity time from rest time by means of the simple amplitude threshold.

Other experimental constraints limit the maximum undisturbed length of the records:

1. Scorpion-spiders only accept living food such as crickets or moths. One cannot readily use feeding intervals (necessary about every 2 weeks) for period evaluation, because the motions of the prey animals are recorded as activity indistinguishable from that of the spider.
2. Longer experiments are often interrupted by molting of the animals.

Obviously, short records complicate a reliable estimation of τ , α and ϱ .

Generally speaking, the problem with which we are confronted is to detect periodic signals hidden in *noise*. This is neither a new nor a specifically biological problem. Early mathematical methods had been developed especially to solve geophysical problems. In recent years advanced methods have become necessary tools in space communication. Today, among the most commonly used methods are Fourier Analysis, the Auto- and Crosscorrelation techniques and Periodogramm Analysis. The textbook of Whittaker and Robinson (1965) provides a good access to the older literature, Halberg (1969) reviews applications in biological and medical research.

Although the problem of the evaluation of a single (average) period seems to be simple, these methods require extensive calculations. Nevertheless, even having done these calculations interpretational problems remain because the question of confidence has not been adequately answered. Perhaps these are the main reasons for the fact that quantitative analytical methods have not yet been used to a greater extent in determining the parameters of circadian rhythms.

In recent years access to electronic computers has continued to improve. Therefore, the need for extensive calculations should no longer be prohibitory.

Additionally the speed of computers makes it possible to improve the analytical methods, especially towards a reduction of possible misinterpretations.

The aim of this paper is to describe an advanced computer-aided method for the evaluation of τ , α (and ϱ) and to discuss it using realistic examples. The locomotor activity records used for this study contain critical cases in which the simple graphical methods fail.

2. Experimental Equipment and Data Acquisition

The activity data have been recorded by an Actograph which was described as "Wippe II" by Beck (1972). It is a circular needle-supported balance. Its motions are transformed into on/off-pulses by a sieve-like aperture which interrupts a light beam. The pulses are summed and printed out at half-hour intervals by the counter (ELMEG ZDG IV).

The experiments were performed with scorpion-spiders of the species *Admetus pumilio*. Their activity behaviour and biology has already been treated by Beck 1972, Beck and Görke 1974, Weygoldt (1972 a, b). Throughout the experimental time of nearly 4 months the animal lived within the Actographs. The temperature was 25 C and the relative humidity greater than 90%. At intervals of 9–18 days crickets were introduced as prey animals for 2 days.

3. Data Processing

All computations have been performed by a digital computer (PDP12 of Digital Equipment Corporation, Maynard USA). The computer programs were written in FORTRAN II (special version of the manufacturer). The activity records obtained from the printing counter were fed in only once via the console typewriter and stored on computer tape. All data for further analyses were derived from this tape.

We have applied a method based on the Periodogram principle (Schuster 1898, Whittaker and Robinson 1924, Enright 1965) for the detection of periodic components in the activity records. Our principal aim in improving this method was to overcome problems of misinterpretation which remain with classical periodogram analysis (see Enright 1965). Therefore, we have added both a confidence limit to separate the "true" peaks of the periodogram from random fluctuations (see 3.2) and a simple analysis of homogeneity (see 3.3). The latter was added to avoid the acceptance of pseudo periods, for instance of subperiods standing in a rational relation to the main period.

Beyond that we have applied a new method to evaluate activity time α and its phase. This method which is based upon intermediate results of the periodogram algorithm also works well with critical records (see 3.4).

3.1 The Periodogram

Periodogram analysis can be based on the following reasoning. If one cuts a record containing *purely* periodic activity of period τ into sections having the length of the period, all sections will be identical and consequently equal to the ensemble average. However, if one chooses a section length not equal to τ , the sections will differ from one another and from their average. Thus, differences between sections and their average can be used as an indicator for whether the section length corresponds to the true period of the record or not. Naturally, this approach can be extended to arbitrary activity records. Fig. 1 (row 1)

shows an example of a record which is not purely periodic (actually generated by computer to test the method). For a more concise description of the periodogram analysis some new terms have to be introduced: the average activity course is called *profile activity*, its periodic continuation (with *trial period p*) *reference activity*.

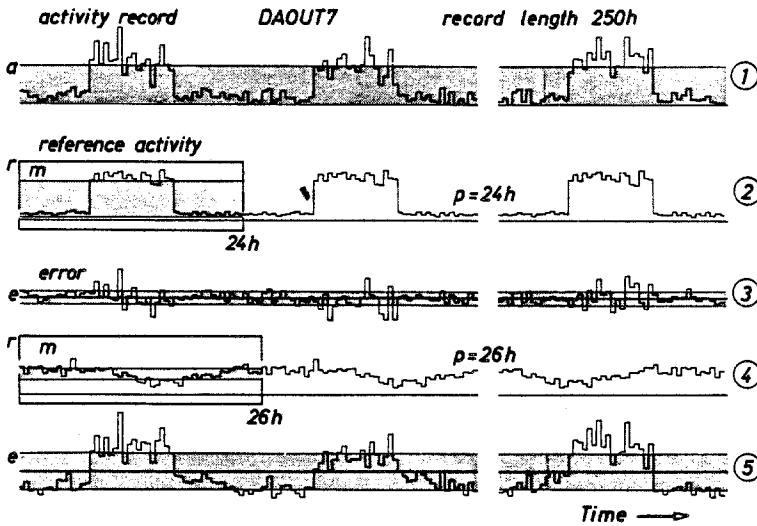


Fig. 1. Explanation of the Periodogram method. ① computer-simulated activity record (DAOUT7); ② profile activity m (within the frame) and reference activity r for a trial period $p=24$ h; ③ error signal = difference between ① and ②; ④ and ⑤ same signals as in ② and ③ but for $p=26$ h (bad estimate). Shaded bands mark the range of ± 1 standard deviation about the mean

In the example of Fig. 1 the second row shows the reference activity r for the (truly estimated) trial period (p) of 24 hours. The frame encloses the profile activity m . The difference between activity a and reference activity r , the error signal e , does not vanish due to the random portions of a , but its standard deviation s_e (marked by the shaded band) becomes much smaller than that of the activity itself (s_a). In the last 2 rows the same signals are shown for a trial period of 26 hours, obviously a bad estimate: the cluster within the profile activity practically disappears and, therefore, the standard deviation of the error signal increases drastically.

If one applies the Schwartz inequality to the second-order moment of m it can be shown easily that s_e cannot become greater than s_a , where s_e approaches this upper limit only for an infinitely long record not containing a periodic component of period p . On the other hand s_e becomes zero only with a purely periodic record (period τ) for $p=\tau$.

Therefore, the definition

$$q(p) = \sqrt{1 - \frac{s_e^2}{s_a^2}} \quad (e \text{ depends on } p!) \quad (1)$$

gives an appropriate measure of the extent to which the record contains a periodic component with period p . Obviously we have

$$0 \leq q(p) \leq 1, \tag{1 a}$$

where $q(p) = 1$ corresponds to the purely periodic activity of period p . Naturally, the definition (1) is not the only one having these properties.

If one evaluates $q(p)$ systematically varying the trial period one obtains some kind of "tuning curve", the periodogram.

In most applications the record is given as a sequence of samples a_j ($j = 1, 2, \dots, L$) which, for instance, have been taken at intervals of 1/2 or 1 hour. For such cases eq. (1) can be written explicitly:

$$q(p) = \sqrt{1 - \frac{\sum_{j=1}^{np} (a_j - r_j)^2}{\sum_{j=1}^{np} (a_j - \bar{a})^2}}. \tag{2}$$

Since (2) only holds for integer p , the true period τ (if any) is implicitly supposed to be a multiple of the sample interval. The integer n gives the number of repetitions in the reference activity. It is chosen as $n = \text{integer part of } (L/p)$. Therefore, only few samples at the end of the record are neglected for the evaluation of $q(p)$. The total average activity \bar{a} is calculated from

$$\bar{a} = \frac{1}{np} \sum_{j=1}^{np} a_j. \tag{2 a}$$

Eq. 2 defines $q(p)$ as a measure of similarity between the record and reference activity r . It has to be mentioned that this is not the only interpretation of the periodogram approach. In fact, most justifications given in the literature are based on the standard deviation of profile activity m . For example, using our symbols the periodogram formula given by Whittaker and Robinson can be written as:

$$q(p) = \sqrt{\frac{\frac{1}{p} \sum_{i=1}^p (m_i - \bar{a})^2}{\frac{1}{np} \sum_{j=1}^{np} (a_j - \bar{a})^2}}. \tag{3}$$

The values m_1, m_2, \dots, m_p of the profile activity are calculated from

$$m_i = \frac{1}{n} \sum_{k=1}^n a_{i+(k-1)p} \tag{3 a}$$

Their mean \bar{m} and the total mean \bar{a} (s. eq. 2 a) are identical. Enright (1965) applied the same formula but omitted the standardizing denominator.¹

¹ This seems not convenient because the denominator is not quite independent of p .

In fact, by use of simple algebraic rules it can be shown that (2) and (3) will give the same result.

Finally, it has to be mentioned that one can also interpret $q(p)$ as a measure of correlation between the given record a and reference activity r (samples r_j ; $j=1, \dots, np$), since

$$q(p) = \frac{\sum_{j=1}^{np} (r_j - \bar{a})(a_j - \bar{a})}{\sqrt{\sum_{j=1}^{np} (r_j - \bar{a})^2 \cdot \sum_{j=1}^{np} (a_j - \bar{a})^2}} \quad (4)$$

The right-hand side of eq. (4) is the common formula for the correlation coefficient, if one takes into account that both data sets possess equal means ($\bar{r} = \bar{a}$). Because r is calculated from a the correlation coefficient cannot become negative. Therefore, eq. (4) is not inconsistent with (1 a).

For our analysis we used eq. (3) as far as this was possible regarding its constraints (integer p , gapless records). Because some records had gaps due to feeding times and malfunction of the recording apparatus we have developed an extension of (3) which enabled us also to analyse such records (see appendix). For non-integral values of p (e.g. 47.3 half-hour recording intervals) we computed $q(p)$ following a rounding scheme already proposed by Whittaker and Robinson.

3.2 Significance of q -Values

Since q is a sample function, it will not become exactly zero even when the record can be regarded as a realisation of a purely random process without any periodic component. To facilitate a discrimination between such spurious q 's and others resulting from real periodic components, an upper limit for these random fluctuations should be known. For given analysis parameters (n, p), it can be stated in the form of a confidence limit q_S below which q is expected with a probability of $S\%$. Subject to the more theoretical constraint of Gaussian distributed activity we have found:

$$q_S = \sqrt{\frac{F_S(f_1, f_2)}{\frac{p(n-1)}{p-1} + F_S(f_1, f_2)}} \quad (p \text{ integer}). \quad (5)$$

In (5) $F_S(f_1, f_2)$ is the corresponding *fractile* of the F -distribution with the 2 *degrees of freedom*

$$f_1 = p \text{ and } f_2 = np. \quad (5a)$$

This fractile can be taken from the tables in nearly all textbooks (e.g. Sachs 1969, chapter 153). However, for high values of f_1 and f_2 as given here the approximate formulas of Hald (1965) also proved to be sufficient.

Fig. 2 shows for $S=95\%$, the dependence of q_S on the analysis parameters p and n . Obviously, q_S decreases mainly with increasing numbers of sections. In the

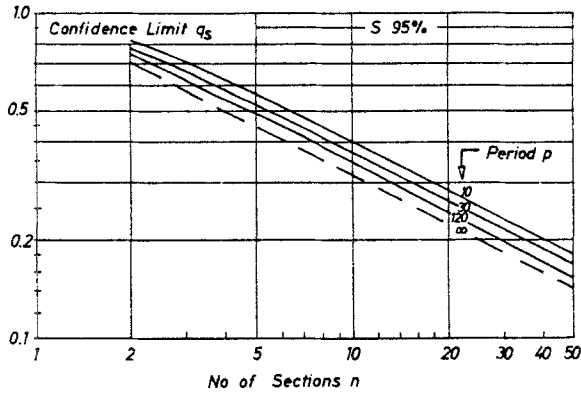


Fig. 2. Confidence limit $q_{0.5}$. A q -value computed from a random, non-periodic record will exceed this limit only with a probability of 5%

(p, n)-range where a periodogram analysis seems meaningful, q_s is subject to changes in proportion to $1/\sqrt{n}$.

In Fig. 3 the periodogram of the simulated activity record DAOUT7 of Fig. 1 is plotted together with the corresponding 95% confidence limit. Besides the expected peak at 24 hours, the periodogram shows a series of other peaks. Their periods stand in a simple rational relation to the 24-hour period as indicated by the fractions in Fig. 3 (see Enright 1965). However, most of these minor maxima do not exceed the confidence limit. If we forget for the moment that the true period is known as it was used when generating the record, we therefore have to interpret only the peaks at the trial periods of 6, 12, 24, and 48 hours.

3.3 Analysis of Homogeneity

A high q -value says very little about the profile activity, namely that its standard deviation is high. However, it says nothing about whether m can be regarded as a real representative of the sections of which it is the average. However,

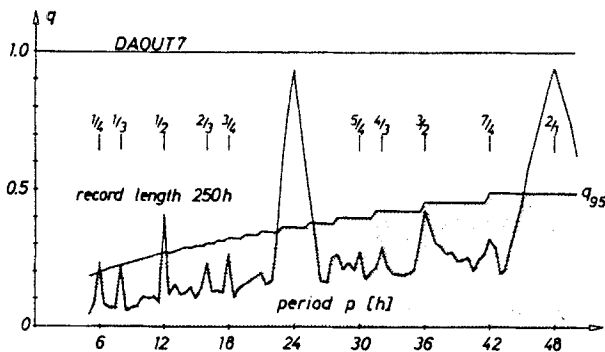


Fig. 3. Periodogram of DAOUT7. Fractions give the relation of peak periods to the basic period of 24 h. Most of the peaks fall below the 95%-confidence limit $q_{0.5}$

that m is representative should be demanded before accepting the trial period of a q -peak as a real period of the activity. That is, we have to ask for *homogeneity*. Therefore, we have added a simple analysis of homogeneity based on total section activity A_k and the efficient section phase L_k (k is the consecutive number of the section; $k = 1, 2, \dots, n$). With activity values assumed as positive numbers we define section activity and section phase by:

$$A_k = \sum_{i=1}^p a_i^{(k)}, \quad (6a)$$

$$L_k = \frac{\sum_{i=1}^p i \cdot a_i^{(k)}}{A_k}, \quad (6b)$$

In (6a, 6b) $a_i^{(k)}$ names the i -th value of the k -th section, i.e. $a_i^{(k)} = a_{i+(k-1)p}$. Obviously, the definition of L_k is similar to that of a centre of gravity. If A_k happened to be zero, we set $L_k = p/2$.

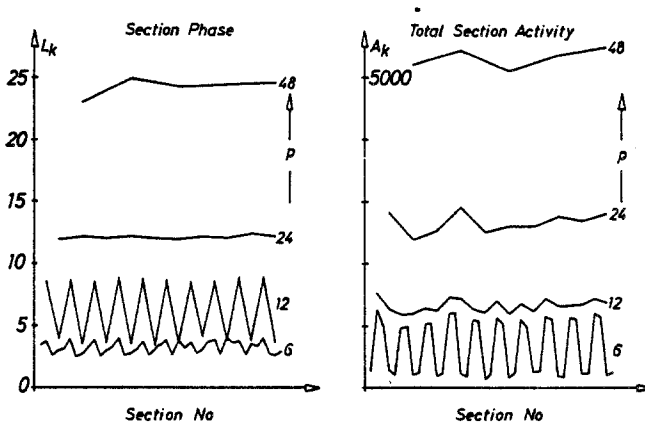


Fig. 4. Analyses of homogeneity for DAOUT7. Because record length is constant (250 h) the number of sections increases with decreasing trial period. For definitions of A_k and L_k see eq. (6a, 6b)

Fig. 4 shows these parameters for the 4 significant trial periods of Fig. 3. As it becomes clear from the oscillations in both total activity and phase the partition is inhomogeneous for trial periods of 6 and 12 hours. Therefore, we have to discard these values of p . For the other periods, 24 and 48 hours, however, neither oscillations nor a trend can be seen. The 48-hour period follows logically from the 24-hour period thus, the latter remains as the only true period.

In analysing natural activity records one seldom finds homogeneity for both parameters. For instance, our records often showed a significant trend of A_k , mostly a decrease with increasing time from the last feeding. If the other conditions (significant q -optimum, homogeneous phase) were met we have nevertheless accepted these periods.

3.4 Computation of α

For reasons already given in the introduction it is difficult to obtain a reliable estimate of activity time α from the record itself. Since the profile activity m suppresses the troublesome non-periodic components of the activity compared to the periodic ones, we think it better to evaluate α (or q) on the basis of m .

The method proposed consists of an approximation of the profile activity for the q -optimal period τ by a rectangular function. Also here the goodness of fit is measured by a least-square criterion, i.e. by the standard deviation of the difference remaining between the profile activity and the approximating function.

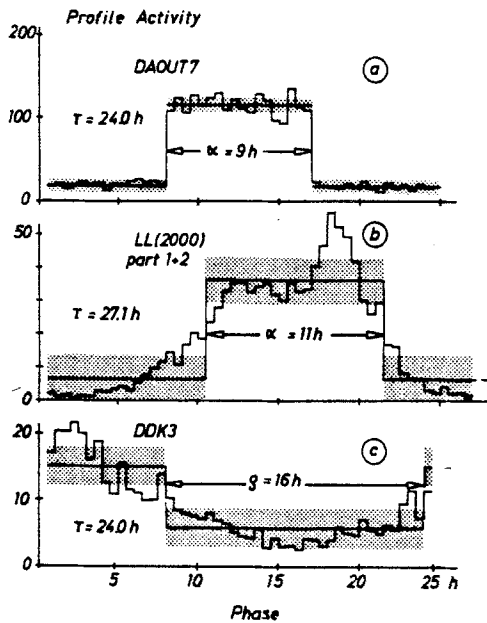


Fig. 5. Computation of α and q . The computer program evaluates the best rectangular approximation of the profile activity for $p=\tau$. Shaded bands mark the standard deviation of the remaining difference. Either α or q can be seen undivided, the duration of the other can be calculated from $\alpha + q = \tau$. Parameters of the records used:

Fig. 5 a. length 500 h, $\tau = 24.0$ h, $q(\tau) = 0.93$;

Fig. 5 b. both parts of LL (2000) in Fig. 6, length 504 h (72 h gap), $\tau = 27.1$ h, $q(\tau) = 0.55$;

Fig. 5 c. DD activity of animal K 3, length 230 h (3 h gap), $\tau = 24.0$ h, $q(\tau) = 0.68$

Fig. 5 shows 3 examples of the approximations obtained. The shaded band marks the remaining standard deviation. For the artificial record DAOUT7 the method provides, as expected, a clear separation into an α having high activities and a low-activity rest time (Fig. 5 a). The remaining standard deviation is very small. We get an activity time of 9 hours (18 half-hour intervals), and for q it holds $q = \tau - \alpha = 15$ hours. The position of the rectangular approximation indicates the phase within the section. The profile activity of Fig. 5 b has been evaluated

from a natural activity record (the two parts named LL (2000) in Fig. 6). Under this experimental condition (continuous light of 2000 lux) the animal is markedly active toward the end of the activity time. Therefore greater differences remain between profile activity and the fitted step function. The profile activity of Fig. 5 c (a different animal in darkness (DD)) is indeed separated by our method into 2 ranges, however, because of the small differences in activity level it does not seem to be justified to use the terms *rest* time and *activity* time.

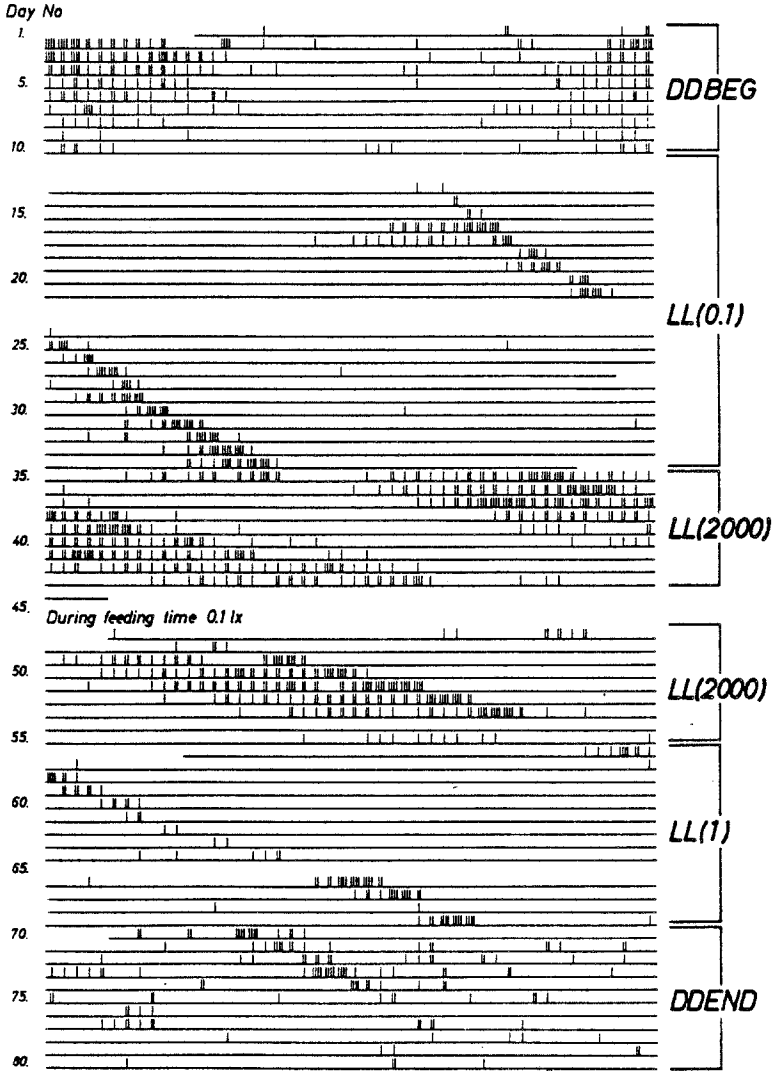


Fig. 6. Actogram of animal K1 under LL conditions. This actogram is not an original record from an event recorder. However, it was reconstructed schematically from the numerical data used for analysis. The only purpose is to give a condensed picture of the data. The absence of line indicates gaps within the record. Analysis gaps at the beginning and end of the record under one experimental condition, e.g. LL (0.1), have been neglected, while internal gaps have been taken into account (see appendix)

4. Biological Application

Fig. 6 represents the activity of a single animal (K 1) over 80 days during which it had been exposed to continuous light of several intensities. The intensity course was the following:

1.—10. day	DD=LL < 10^{-5} lux,	record: DDBEG
11.—34. day	LL of 0.1 lux,	record: LL (0.1)
35.—55. day	LL of 2000 lux,	record: LL (2000)
56.—69. day	LL of 1 lux,	record: LL (1)
70.—80. day	DD as above,	record: DDEND

On days 11/12, 22/23, 44/46 and 65 the animal was fed. During the long feeding pause on days 44/46 the intensity had to be lowered from 2000 lux to 0.1 lux because the unphysiological high intensities interfere with the capture behaviour of the scorpion-spiders. Therefore we had to analyse the record LL (2000) in two parts. (In fact, the analysis showed that the feeding pause led to a notable phase lag.) Thus, we obtained 6 records under the conditions

$$DD - LL (0.1) - LL (2000) - LL (2000) - LL (1) - DD$$

for analysis. Not all of the results can be shown here in detail. We confine ourselves to the two records DDBEG (10 days) and the 22-days long record LL (0.1). Even though the actogram of DDBEG (Fig. 6) shows only a blurred periodic pattern its periodogram (Fig. 7) has a peak well above the confidence limit. The position of its maximum indicates $\tau = 23.7$ hours. In contrast, the periodicity of LL (0.1) is obvious even from the actogram. Its periodogram shows a steep maximum with a period of 24.85 hours. A comparison of the profile activities m shows a distinct contrast. The DD-record DDBEG shows a very long activity time of 7 hours while LL (0.1) concentrates nearly the same total activity within an α of 2 hours. The homogeneity analysis proves (Fig. 7) that the partition can be regarded as homogeneous with respect to the section phases L_k but not to the total section activities A_k . For the latter DDBEG shows a uniform trend to lower activities while the A_k 's of LL (0.1) fluctuate over a wide range.

Some remarks are necessary concerning the form of the periodograms. The broad periodogram of DDBEG could lead to the interpretation that the q -optimum does not result from a unique periodic component within the whole record but only from an average of several periods in different parts of the record. However, this interpretation is inconsistent with the fact that the section phases are nearly constant. The reasoning given for the periodogram (see 3.1) suggests a different explanation of the broad q -maximum, namely that it is simply a consequence of the long activity time and the brevity of the record (234 h). We have tested this suggestion by comparing the periodogram of DDBEG with that of a computer-simulated record containing a unique period.

We started the simulation from the reference activity evaluated from DDBEG at its optimum period. We then multiplied the signal by positive, independent random numbers with a mean of 1 and a variance calculated from the peak value $q(\tau)$ of the DDBEG-periodogram. (The distribution type was chosen as

lognormal.) This operation yielded a simulated record which was equal (in a statistical sense) to DDBEG in respect of both profile activity and the parameters ($\tau, q(\tau)$) of the peak of its periodogram.

Fig. 8 shows the periodograms of two simulated records of different length compared to that of DDBEG. Clearly, the periodograms of DDBEG and of the equally long (234 h) simulated record are the same, if we neglect some small

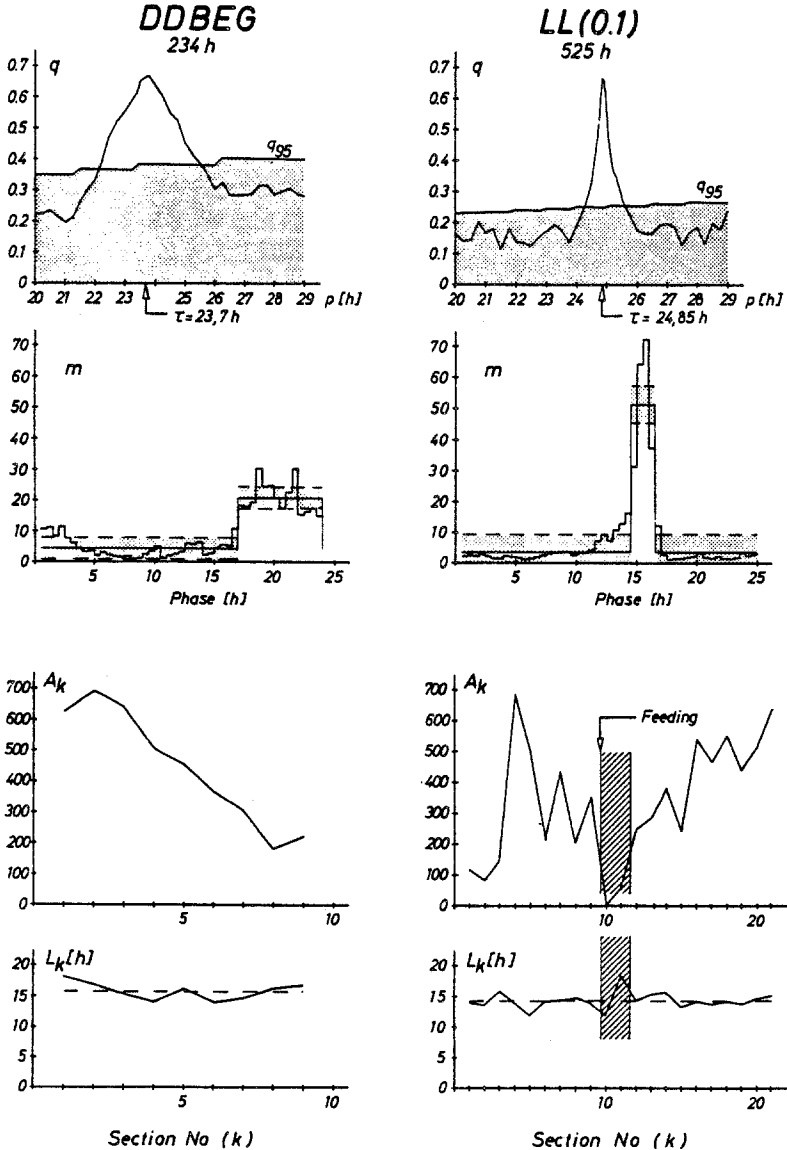


Fig. 7. Analysis of DDBEG and LL(0.1). For both records are shown: the periodogram (q), profile activity (m) at optimum period (τ), the total section activity (A_k), and the section phase (L_k)

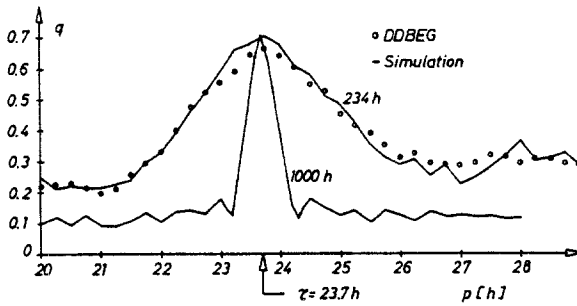


Fig. 8. Comparison of DDBEG with simulated data. This is to show that the wide maximum in the DDBEG periodogram results from the relatively long activity time and the short record length but *not* from a trend or instability in periods

random fluctuations. The increased simulation length of 1000 hours leads to a significantly narrowed peak. Therefore, we can conclude, that the broad peak in the periodogram of DDBEG can be reduced to just the profile activity course and the length of the record.

All 6 records of Fig. 6 led to periodograms with single significant peaks, and could be regarded as homogeneous, at least with respect to the section phases. Fig. 9 summarizes the results concerning α and τ . Generally, the period increased with light intensity. For α , the result seems more complex. But, if we neglect for the moment the DDBEG-value (No. 1), we can obtain from the diagram constant activity times of 2 hours for all intensities up to 10 lux. We get a different value (9.5 hours) only for the unphysiological intensity of 2000 lux. A reasonable interpretation of the high α for DDBEG is, that the animal was put into the actograph only 6 hours before starting to record its activity. Possibly, the animal

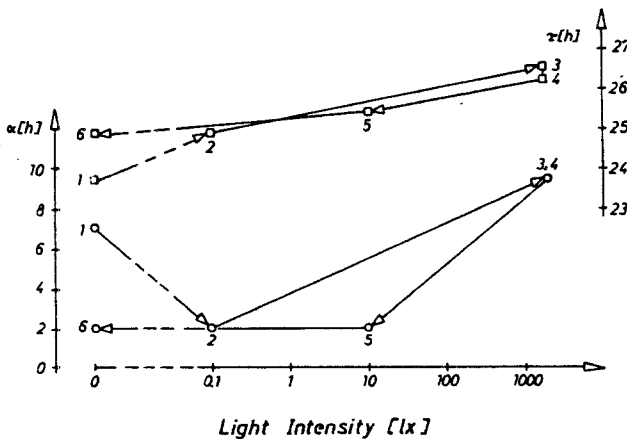


Fig. 9. Summary of the (τ , α)-analysis. Periods (□) and activity times (○) for animal K I under several LL-conditions. Numbers indicate the sequence in which the intensities had been varied

had explored its new environment. This interpretation is supported by the nearly monotonous decrease of the total section activity (A_k) with increasing experimental time (Fig. 7).

We are indebted to Mr. W. Mittmann for an early version of the computer program, to Miss U. Börger who took care of the experiments and performed most of the computer analysis, to Mrs. B. Gunkler for the drawings and for permanent assistance with the preparation of the manuscript, and to Dr. D. J. Miller for reviewing the English text.

Appendix

The Evaluation of Periodograms from Records Containing Gaps

Gaps within the record bring an uncertainty into the periodogram evaluation. Therefore, a periodogram formula appropriate to gap-containing records must result in q -values which reflect this uncertainty, i.e. it has to lead to smaller q -peaks.

One can imagine several models for filling up the gaps, for instance by randomly chosen values. We started from eq. (3)

$$q(p) = \sqrt{\frac{\frac{1}{p} \sum_{i=1}^p (m_i - \bar{a})^2}{\frac{1}{np} \sum_{j=1}^{np} (a_j - \bar{a})^2}} \quad (3)$$

and estimated the total variance in the denominator from the L_p^* ($\leq np$) given values a_j by

$$\bar{a} := \frac{1}{L_p^*} \sum_{j=1}^{np} a_j$$

$$\frac{1}{np} \sum_{j=1}^{np} (a_j - \bar{a})^2 := \frac{1}{L_p^*} \sum_{j=1}^{np} (a_j - \bar{a})^2.$$

\sum^* indicates that the sums are only extended over the j 's with given a_j . When computing the profile activity m_i which was needed for the nominator of (3), we fill up all gaps by the mean value \bar{a} , that is we set:

$$m_i := \frac{1}{n} \left((n - n_i) \bar{a} + \sum_{k=1}^{n_i} a_{i+(k-1)p} \right).$$

In this equation n_i is the number of activity values which are given for the evaluation of m_i , where $n_i \leq n$. If we name the profile activity, which we could compute from the *non-gap* values, as m'_i , that is:

$$m'_i = \frac{1}{n_i} \sum_{k=1}^{n_i} a_{i+(k-1)p},$$

then we can also write the q -formula for records containing gaps as

$$q(p) = \sqrt{\frac{\frac{1}{p} \sum_{i=1}^p \left(\frac{n_i}{n}\right)^2 \cdot (m'_i - \bar{a})^2}{\frac{1}{L_p^*} \sum_{i=1}^{np} (a_j - \bar{a})^2}}$$

This formula and (3) are identical for gapless records. If the record does contain gaps the periodogram still reaches its maximum for a purely periodic activity. However, its amplitude depends on both the relative number of gaps and their distribution.

At best q can reach

$$q_{\max} = \frac{L_p^*}{n p}.$$

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Dr. G. J. Dörrscheidt
 Prof. Dr. L. Beck
 Lehrstuhl für Allgemeine Zoologie
 Ruhr-Universität Bochum
 Postfach 2148
 D-4630 Bochum
 Federal Republic of Germany