Running Activity Patterns of Females and Last Larval Instars of the Cockroach *Leucophaea maderae*

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Virgin females of *Leucophaea maderae* reveal a circadian rhythm in their locomotor activity which is superimposed by the ovarial cycle. Locomotor activity of last larval instars does not exhibit a circadian pattern.

Locomotor activity of cockroaches, especially *Leucophaea maderae*, has frequently been used in circadian rhythm research. Most of the work, however, has focused on adult males [1], whereas females were mentioned to show generally a more erratic pattern [2]. Activity records of female *Periplaneta americana* were discussed as being correlated with the reproductive cycle [3]. Only one recent study compared in more detail the activity rhythms of female and male adults and of the first 4 larval instars of *L. maderae* [4]. Additional results on females and last larval instars are reported here.

Locomotor activity was recorded in running-wheels under continuous red light (up to 40 μW/cm²) and constant temperature (28 °C ± 1 °C) [5]. Temporal alterations in the amount of activity instead of a continuous pattern characterize the actograms of adult virgin females of *L. maderae* (Fig. 1). Still, a circadian free-running period can be detected, since the sections of high activity fit a straight line connecting the onsets of activity. About 7 – 10 days after the last moult a circadian activity pattern occurs for 5 – 15 cycles. Subsequently females stay inactive for 4 – 5 weeks until another section of activity follows, and so on. About 8 – 10 days after activity ceased an empty ootheca was often found in the running wheel. As insects frequently feed on the ootheca [6], it may not have been discovered in all possible cases. Female cockroaches release pheromones related to their sexual cycle [7, 8], and the first maximum of release occurs during the second week following the imaginal moult [7]. That coincides with the first section of locomotor activity in our data. Virgin females of *L. maderae* ovulate every 4 – 5 weeks, but longer intervals were also found [6]. This corresponds again to the sections of high activity in our results. The locomotor activity pattern in female *L. maderae* can therefore be traced back to a superposition of the circadian rhythm and the ovarial cycle.

Last larval instars of *L. maderae* are mainly active during the dark part of an LD-cycle. In constant conditions, however, rhythmicity disappears. Some regular patterns may occur for several days, but they are fequently interrupted by discontinuities such as phase jumps or period changes (Fig. 2). To determine if any periodicity underlies such patterns, a time series analysis of four arbitrarily selected actograms (average time recorded: 37 days) was performed by using TIMESDIA [9]. Fig. 3a shows the periodogram of Fig. 2a. No significant general period-length in the circadian range was discovered. In two cases a significant semi-circadian component was found; an example is given in Figs. 2b and 3b. The estimated period-length is indicated as 11.65 h. Yet, as shown in the phase diagram of the complex demodulation (Fig. 3c), the ryhthm is not stable and not continuously present in the time series: the instantaneous phase of the periodicity under investigation is not a straight line (for more details about complex demodulation we refer to [10]).

These findings differ in some respects from results by Page and Block [4], who reported circadian rhythms in the first larval instars of *L. maderae,*

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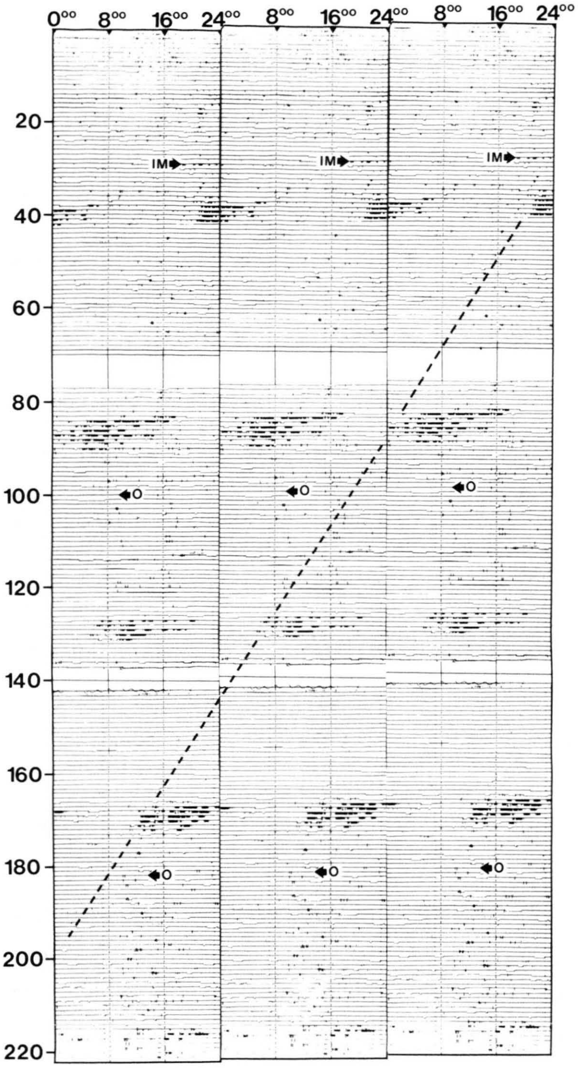


Fig. 1. Actogram of a female *Leucophaea maderae* over 221 days in constant conditions. The continuous recording is cut into 24 h sections, and subsequently arranged underneath each other. The actogram is reproduced three times to point out the circadian component (dashed line). IM indicates imaginal moult, o discovery of an ootheca in the running-wheel. On days 69–76 and 137–142 the recorder failed. *Abscissa:* hours of day; *Ordinate:* days of experiment.

Fig. 3. Time series analysis of the actograms shown in Fig. 2 by using TIMESDIA. a) Periodogram of actogram Fig. 2a. b) Periodogram of Fig. 2b, and c) phase diagram of the same actogram demodulated at period-length 11.65 h. *Abscissa:* of periodogram: period-length in hours; of phase diagram: subsequent hours of actogram. *Ordinate:* of periodogram: intensity, *i. e.* the extent q to which the time series contains a periodic component with period p $0 \leq q(p) \leq 1$; of phase diagram: instantaneous phase of periodicity at which we demodulated (*cf.* [10]).

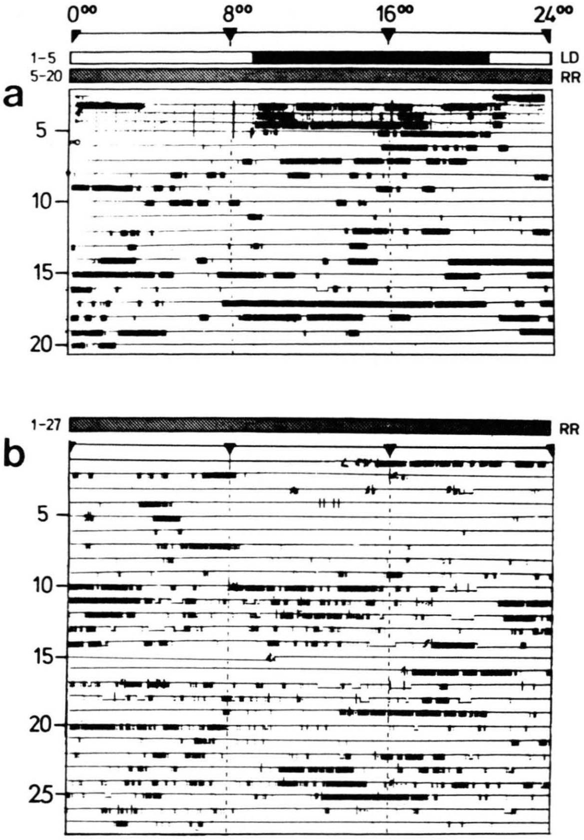
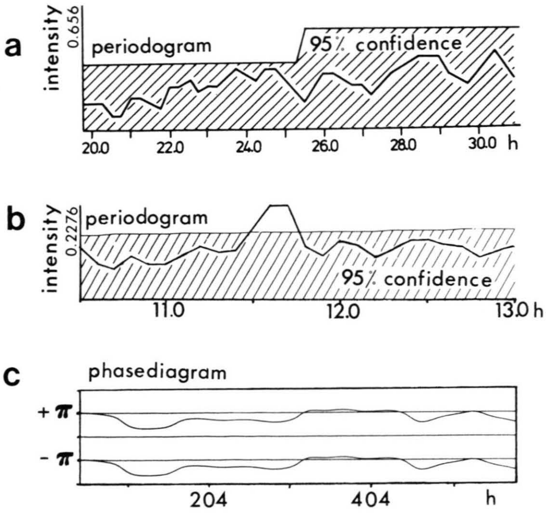


Fig. 2. Actograms of last larval instars. a) Day 1–5 LD 12:12, day 5–20 continuous red light. b) Day 1–27 continuous red light. *Abscissa:* hours of day. *Ordinate:* days of experiments.



though sometimes discontinuous or not very pronounced. Both sets of results may, however, be explained by a stochastic model without the assumption of a clock mechanism [11]: its simulations show patterns similar to those presented here, as well as to the rhythmicity found by Page and Block. Since adult males do show a circadian rhythm which is obviously controlled by an oscillatory mechanism [12], *L. maderae* would be another example for different mechanisms underlying circadian rhythms in different developmental stages [13]. To prove such coherence requires further investigation.

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