With best wishes and many thanks John

DERU, DUNES, NAMIB
P/copy 07/04 Mary

9429

Journal of Arid Environments (1990) **19**, 317–324

Thermal ecology and behaviour of *Physadesmia globosa* (Coleoptera: Tenebrionidae) in the Namib Desert

J. L. Cloudsley-Thompson*

Accepted 30 April 1990

Of 2850 *Physadesmia globosa* counted at the Desert Ecological Research Unit of Namibia, Gobabeb, 67% were found beneath a large *Acacia erioloba* and two large *Euclea pseudebenus* beside it; the remainder in the open or beneath smaller trees. There was no tendency for the beetles to be in the open more at times when air temperatures were lower than higher. Wind speed had no effect on activity. The insects buried themselves, or retreated beneath rocks and stones at night. Of 1914 beetles sexed, 63% were male, 37% female. Vision is much used in day to day activity. Although not a fog-basking species, *P. globosa* sucks moisture from damp sand. This may shed light on the evolutionary origin of fog-basking in other species. No significant difference was recorded between the body temperatures of beetles selected at random, and those of geckos, *Rhoptrophis afer*, captured on nearby rocks at the same time of day. A population of some 60,000 km^{-2} was calculated around a point in the Kuiseb River bed. It is suggested that diurnal activity in *P. globosa* may be related to the cold nights and the enhancement of metabolic activity. Conclusions based on field observations were confirmed in the laboratory by aktograph experiments on the diurnal rhythm of locomotory activity.

Introduction

Physadesmia globosa (Haag) (Coleoptera: Tenebrionidae) is a day-active, flightless scavenger and detritivore of the dry Kuiseb River bed, Namibia. The rhythm of activity has been investigated in the field by Ferguson (1989) using focal animal sampling. Adult beetles were found to have a bimodal periodicity in summer, with peaks of surface activity during the morning and late afternoon, as previously reported by Wharton & Seely (1982). No clear correlation between ambient temperature and daily levels of activity was obtained by these authors, and some of the highest numbers of beetles were recorded during the period 1600 to 1700 h when the ambient temperature was highest. One of the objectives of the present investigation has been to clarify the rôles of the circadian rhythm and ambient temperature in the chronobiological control mechanism (Applin *et al.*, 1987).

Sexual behaviour is highly conspicuous in *P. globosa* because males follow close behind active foraging females and engage in physical contest with other males for a position immediately behind the females (Marden, 1987). Casual observation suggested that copulation did not take place either as readily or so frequently as claimed. This point was therefore also investigated. In addition, burying behaviour, water intake, and precision of thermoregulation (compared with that of the rock gecko *Rhoptrophis afer*) were also studied.

* Department of Biology (Medawar Building), University College London, University of London, Gower Street, London WC1E 6BT, U.K.

0140–1963/90/060317 + 08 $03·00/0

Methods

Several times daily, at irregular intervals, on 20 days between 6 October and 9 November 1989, the numbers of *P. globosa* were noted on a transect *c.* 10 m wide and *c.* 200 m long at the Desert Ecological Research Unit of Namibia, Gobabeb (23° 34′S, 15° 03′E). Of this transect, *c.* 100 m were on open gravel plain, *c.* 75 m beside 20 small trees (*c.* 2–3 m high) and *c.* 25 m beside three large trees. Most of these trees were *Euclea pseudebenus,* but one of the three largest was an *Acacia erioloba.* The greatest numbers of beetles were invariably recorded beneath this, and the two equally large *E. pseudebenus* beside it, at the eastern extremity of the transect. The beetles were counted at intervals of not less than 30–45 min and, when appropriate (Figs 1, 2), the results were lumped to the nearest hour.

Air temperatures and relative humidities were assessed by means of a whirling hygrometer. Whenever variations or fluctuation occurred the maximum temperature was recorded to the nearest 0·5°C. Black bulb temperatures and radiation were not measured. The temperatures on the surface of the ground and rocks, as well as the sub-elytral temperatures of beetles and cloacal temperatures of rock geckos (*Rhoptrophis afer*) were measured with a Bailey Instruments (BAT-12) thermocouple thermometer. Wind speeds were recorded with a cup-type anemometer, and cloud cover was estimated visually. Very close agreement was obtained when these readings were compared with equivalent figures recorded in the adjacent Meteorological Station.

The temperature of the sand in shade closely followed that of the air, usually registering about 2°C above it. I therefore used air temperature rather than shaded sand temperature in the calculation of parameters, while the number of beetles active was also assessed in relation to air temperature measured with the dry bulb of the whirling hygrometer.

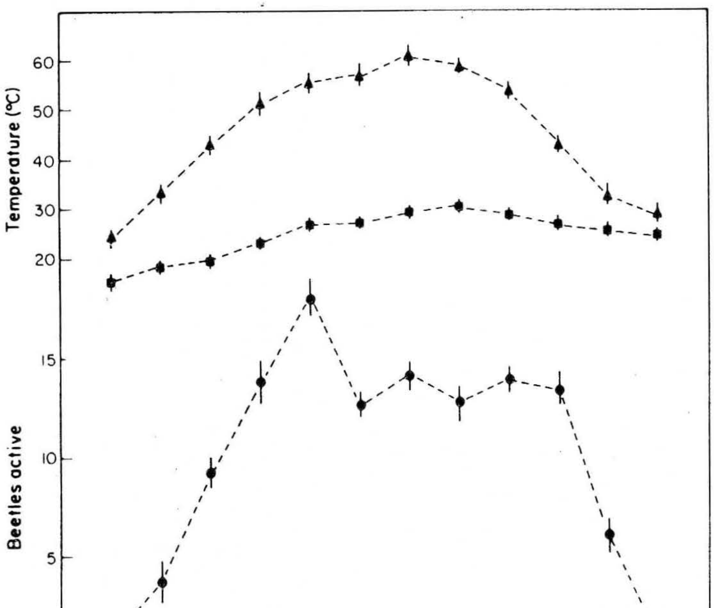

Figure 1. Mean number of *P. globosa* active at hourly intervals throughout the day, in relation to mean ambient air temperatures (■) and mean maximum sand-surface temperatures (▲) at the same times. Vertical bars indicate the standard errors of the means.

The environment (
Research Station had l
watered by hose pip
differently from those

T

The mean numbers of
intervals are shown in
weather when midday
morning air temperatu
(*c.* 1900 h) even when
between rising and fal
numbers have been plo
The peak temperature
numbers were very mu
than when it was rising
retired at dusk, althou
morning, even when l
15°C had been reached

Of a total of 2850 pos
under the 20 small *E.*
two large *E. pseudeben*
Crawford *et al.* (1990).
morning when the tem
morning and the after
compare with 7% of the
30°C, and 23% above 3(

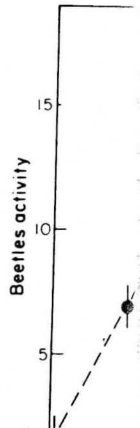

Figure 2. Mean numbers
temperatures on the left, fa
of the means.

The environment of the study area was unnatural in the sense that the trees in the Research Station had been planted on what had originally been open gravel plain, and were watered by hose pipe. Nevertheless, the *P. globosa* there did not appear to behave differently from those in the Kuisib River bed.

Results

The daily cycle of activity and its thermal correlates

The mean numbers of position records of beetles (± standard errors) recorded at hourly intervals are shown in Fig. 1. The cycle of activity tended to become bimodal in warmer weather when midday temperatures exceeded 30–35°C. Activity did not begin until the morning air temperature had reached about 15°C, but the beetles retired around sunset (*c*. 1900 h) even when the air temperature was still considerably above this. The relation between rising and falling ambient temperature on activity is illustrated in Fig. 2, where numbers have been plotted separately when temperatures were increasing and decreasing. The peak temperature each day was reached around 1500 h. As can be seen from Fig. 2, numbers were very much lower, in the range 20–25°C, when the temperature was falling than when it was rising and none were active below 20°C. This suggests that the beetles retired at dusk, although the temperature was still high, but did not reappear in the morning, even when light intensity was considerable, until an air temperature of about 15°C had been reached.

Of a total of 2850 position records of beetles, 16·5% were noted in the open plain, 16·5% under the 20 small *E. pseudebenus* trees and 67·0% beneath the large *A. erioloba* and the two large *E. pseudebenus* next to it. This is in agreement with the conclusions reached by Crawford *et al.* (1990). Of the specimens observed in the open, 19% were counted in the morning when the temperature was below 20°C, 66% between 20 and 30°C, both in the morning and the afternoon, and 14% around midday and above 30°C. These figures compare with 7% of the total when the temperature was below 20°C, 70% between 20 and 30°C, and 23% above 30°C. There was therefore no apparent tendency for the beetles to be

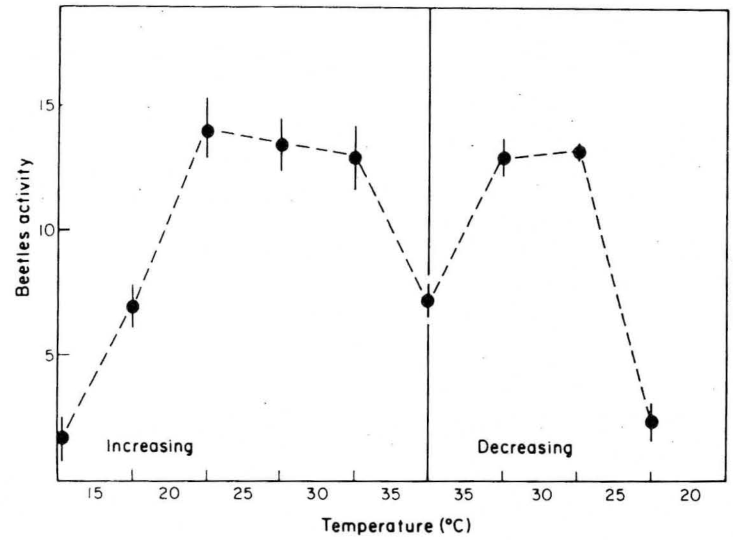

Figure 2. Mean numbers of beetles active in relation to mean ambient air temperatures. Rising temperatures on the left, falling temperatures on the right. Vertical bars indicate the standard errors of the means.

more active in the open when ambient air temperatures were lower. While in the open early in the morning, however, they were usually rather sluggish and in pairs consisting of a male and a female. Later in the day, they were more often solitary and fast moving when in the open.

The mean maximum wind speed recorded throughout the period of study, based on 262 readings made at times when beetles were active, was 6·0 ms^{-1} (range 0–18 ms^{-1}); but no effect of wind on the activity of the beetles was noted.

Burying behaviour

By about 1830 h, most of the beetles had either retreated beneath rocks and stones or buried themselves in the sand. In the Kuiseb River bed there are few alternatives to burial. At the Research Station, some failed to cover themselves completely and left portions of their elytra visible: the majority did not bury themselves more than 1 or 2 cm. In a vivarium only between about 3 and 5 out of 20 would be completely hidden. One male buried itself in gravelly sand to a depth exceeding 2 cm two nights running. In contrast, captive specimens of *Onymacris marginipennis* buried themselves more deeply.

Burial was a rather casual process in *P. globosa*. It was observed most often beneath the large *A. erioloba* and *E. pseudebenus* trees within the transect area. A beetle would dig itself into the sand beneath the dry leaf litter, pressing its hind legs against any small object, such as a stone or twig, that gave mechanical purchase, until only the tip of the elytra was visible. It might remain in this position for as long as 10 or 15 min, by which time the observer could well have assumed it to have finally settled. But then, not infrequently, it would struggle to the surface, hurry away and seek yet another quite distant place in which to rest for the night. Of a number of individuals followed to their nocturnal abodes, and which were found there the following morning, one female wedged herself between two rocks, another into a crack beside a partly buried hose-pipe, others secreted themselves in the sand under detritus, showing opportunistic use of the habitat. The black posteriors of partly hidden beetles were visible early in the morning before the insects had woken. The last to retire for the night appeared usually to be frustrated males that had carelessly lost the females they were following, often as a result of interactions with other males.

Reproduction and sex ratio

Marden's (1987) observations, made in the dry river bed have, in general, been confirmed on the gravel plain to the north. Sometimes two or even three males could be seen following the same female at intervals of 3–5 cm. Often a male would close up with the female and grasp her with his first pair of legs, running behind her with only the second and third pairs on the ground. Such behaviour was not mentioned by Marden (1987): nor did copulation, let alone mounting, appear to take place anything like as frequently as he noted. Furthermore, contrary to his claim, males and females sometimes fed side by side. Naturally, it would be difficult for a male to feed and copulate simultaneously because, while mating, its food lay on the ground while the male was mounted on the female's back. Reproductive behaviour was apparent from the moment the beetles appeared. They did not invariably feed first and mate afterwards as Marden (1987) found. On Jebel Marra, Sudan, *Adesmia variolis* begins its active day by copulating and afterwards concentrates on feeding (Cloudsley-Thompson, 1967).

Of 1914 beetles sexed, 63% were male, 37% female. This indicates either greater activity on the part of the male sex in this species, or a skewed sex ratio. No evidence was obtained that males appeared either earlier or later in the day than the females, or that their numbers decreased more or less rapidly.

Vision is apparently much used in day to day activities, such as following a female or avoiding capture. Although seldom disturbed by vibrations caused by stamping, unless very close, the beetles were stimulated by the movement of a finger at 5 cm or when approached to a distance of 3 m or so.

Water intake

Although not a 'fog-basking' species (Louw, 1972; Hamilton & Seely, 1976), *P. globosa* was observed to emerge from the sand at the edge of the dunes on foggy mornings and feed upon sodden detritus. The beetles were covered with sand which adhered to their wet integuments and unbalanced them by its weight. They were very lethargic. It is not improbable that both they and fog-basking *Onymacris plana* are stimulated by sudden drops in temperature, as are other arthropods such as millipedes (Cloudsley-Thompson, 1951). This may engender their emergence so that the moisture emanating from the fog can be exploited. The head downward stance, adopted by both species of beetle when sucking moisture from damp sand would ensure that drops of moisture condensing on the body would flow towards the mouth. Such may be an explanation of the evolution of this adaptive behaviour in *O. plana*. Water balance and osmotic regulation in *P. globosa* have been studied by Naidu & Hattingh (1988).

Thermoregulation in P. globosa *compared with the rock gecko* Rhoptrophis afer

In order to compare thermoregulation in *P. globosa* with that in a day-active reptile, the body temperatures of beetles selected at random were compared with those of rock geckos (*Rhoptrophis afer*) captured nearby. The beetles were able to move into sunshine or the shade of a tree; the geckos to shuttle between boulders or crevices in the rock. Beetle temperatures were assessed by inserting a thermocouple into the sub-elytral cavity through a small hole pierced through one elytron. The cloacal temperatures of the geckos were measured with the same thermocouple, as soon as possible afterwards. The mean weight of *P. globosa* was 0·75 g, that of *R. afer* 2·8 g (range 1·5–4·5 g). Such differences would invalidate comparison except when the ambient temperatures were relatively stable. Measurements were made on nine different afternoons when air temperatures ranged between 24 and 33°C (mean 27·2°C), sand temperatures (in sun) between 27 and 62°C (mean 44·3°C) and rock temperatures (in sun) between 27 and 49°C (mean 32·5°C).

Despite differences in weight, the mean body temperature of the beetles was 31·7°C (±0·60°C S.E.) ($n = 19$), that of the geckos 31·3°C (±0·51°C S.E.) ($n = 19$). There was, therefore, no significant difference between the body temperatures recorded in the beetles and the geckos. In general, the geckos tended to appear earlier in the morning than did the beetles, and to retire later.

Movements and population

P. globosa travels considerable distances quite rapidly. One of 10 marked with paint and released on 7 October at the extreme west of the transect was recovered the following day at the extreme east, a distance of 200 m. Another, released at the same time, was found 23 days later at the place of release and a third, 19 days later, in a pitfall trap in the Kuiseb River bed *c.* 500 m south. Of a total of 1000 *P. globosa*, marked and numbered for a population study by Uri Werner before being released in the Kuiseb River bed, four different individuals were observed in the transect during the first 10 days, often on more than one occasion. In all, of a total of 2850 beetle records, 67 were of beetles that had previously been numbered and released. This suggests a population of some 45,000 beetles in the region encompassing the transect and the river bed. That is, in an area of about 0·75 km^2 (a circle of radius 500 m around the point of release), or 60,000 km^{-2}— assuming movement was equal in all directions from the place at which the beetles were released.

In the Namib Desert, particularly on the dunes and in the beds of the rivers, day-active beetles tend to be more numerous than night-active species (Crawford *et al.*, 1990). On the other hand, in the Great Palaearctic desert, nocturnal and crepuscular species predominate (Cloudsley-Thompson & Constantinou, 1985). This difference may be accounted for by the less extreme environmental conditions and the regular occurrence of moisture in the form of dew and fog in the Namib. At the same time, the nights are generally too cold there to reward locomotory activity (Crawford *et al.*, 1990). Few animals were found in the study transect after dark—a large *Prosolpuga schultzii* (Solifugae) attracted to light, *Parastizopus* sp. (Tenebrionidae) and *Scarabaeus* sp. (Scarabaeidae).

Warmest thanks are due to all the people who helped me in this work, and especially to Dr Mary Seely, Director: Desert Ecological Research Unit of Namibia, Linda and Francois Malan, my wife Anne Cloudsley who joined me in making the observations, and Magda Nel for her incredible skill in catching rock geckos. The Namibia Department of Agriculture and Nature Conservation gave permission for me to work in the Namib Naukluft Park, and the research was supported by a Leverhulme Emeritus Fellowship for which I am most grateful.

References

Applin, D. G., Cloudsley-Thompson, J. L. & Constantinou, C. (1987). Molecular and physiological mechanisms in chronobiology—their manifestations in the desert ecosystem. *Journal of Arid Environments*, **12**: 187–197.

Aschoff, J. (1961). Exogenous and endogenous components in circadian rhythms. *Cold Spring Harbor Symposia on Quantitative Biology*, **25** (1960): 11–28.

Cloudsley-Thompson, J. L. (1951). On the responses to environmental stimuli and the sensory physiology of millipedes (Diplopoda). *Proceedings of the Zoological Society of London*, **121**: 253–277.

Cloudsley-Thompson, J. L. (1967). Altitude and faunal distribution on Jebel Marra. *Sudan Notes and Records*, **48**: 133–140.

Cloudsley-Thompson, J. L. (1979). Adaptive functions of the colours of desert animals. *Journal of Arid Environments*, **2**: 95–104.

Cloudsley-Thompson, J. L. & Constantinou, C. (1985). Biological clocks in desert beetles (Tenebrionidae), with special reference to *Erodius octocostatus* Peyerimhof in Kuwait. *Journal of the University of Kuwait (Science)*, **12**: 237–243.

Constantinou, C. (1980). Entrainment of the circadian rhythm of activity in desert and forest inhabiting scorpions. *Journal of Arid Environments*, **3**: 131–139.

Crawford, C. S., Hanrahan, S. A. & Seely, M. K. (1990). Tenebrionid detritivores: habitat selection and resource use in a Namib riparian woodland. In: Seely, M. K. (Ed.), *Current Research on Namib Ecology—25 Years of the Desert Ecological Research Unit.* Transvaal Museum Monograph No. 8 (in press).

Ferguson, J. W. H. (1989). Summer activity patterns of the riparian desert beetle *Physadesmia globosa*. *Madoqua*, **16**: 9–13.

Hamilton, W. J. III & Seely, M. K. (1976). Fog basking by the Namib Desert beetle *Onymacris unguicularis*. *Nature*, **262**: 284–285.

Louw, G. N. (1972). The rôle of advective fog in the water economy of certain Namib desert animals. *Symposium of the Zoological Society of London*, **31**: 297–314.

Marden, J. H. (1987). In pursuit of females: following and contest behaviour by males of a Namib Desert tenebrionid beetle, *Physadesmia globosa*. *Ethology*, **75**: 15–24.

Naidu, S. G. & Hattingh, H. (1988). Water balance and osmoregulation in *Physadesmia globosa*, a diurnal tenebrionid beetle from the Namib Desert. *Journal of Insect Physiology*, **34**: 911–917.

Wharton, R. A. & Seely, M. K. (1982). Species composition of and biological notes on the Tenebrionidae of the lower Kuiseb River and adjacent gravel plain. *Madoqua*, **13**: 5–25.

n an area of about 0·75
000 km^{-2}— assuming
beetles were released.
of the rivers, day-active
ord *et al.*, 1990). On the
cular species predomi-
e may be accounted for
rence of moisture in the
generally too cold there
were found in the study
ed to light, *Parastizopus*

nd especially to Dr Mary
Francois Malan, my wife
el for her incredible skill in
Nature Conservation gave
earch was supported by a

iolecular and physiological
cosystem. *Journal of Arid*

ian rhythms. *Cold Spring*

il stimuli and the sensory
ciety of London, **121**: 253–

Jebel Marra. *Sudan Notes*

desert animals. *Journal of*

clocks in desert beetles
ıhof in Kuwait. *Journal of*

ivity in desert and forest

tritivores: habitat selection
Ed.), *Current Research on*
svaal Museum Monograph

desert beetle *Physadesmia*

b Desert beetle *Onymacris*

of certain Namib desert

viour by males of a Namib

ı in *Physadesmia globosa*, a
'hysiology, **34**: 911–917.
d biological notes on the
Iadoqua, **13**: 5–25.

Appendix

Experimental evaluation of the circadian rhythm of *P. globosa*

C. Constantinou

Method

The locomotory activity of individual beetles was recorded by the aktograph apparatus previously described (Constantinou, 1980). The beetles were placed in crystallising dishes with lids made of two sheets of copper electrically insulated from one another. The upper sheet was connected to a 24 V D.C. power supply, the lower to a multi-channel event recorder. Content was made or broken by steel pins suspended from the upper sheet of the lid, and passing through the lower sheet. When the beetles moved inside the cages, they deflected these pins so that they made contact between both sheets of the lids, thus completing the electric circuit incorporating the activity cages, power supply and event recorder. The beetles in the crystallising dishes were either exposed to cycles of 6·5 h light:

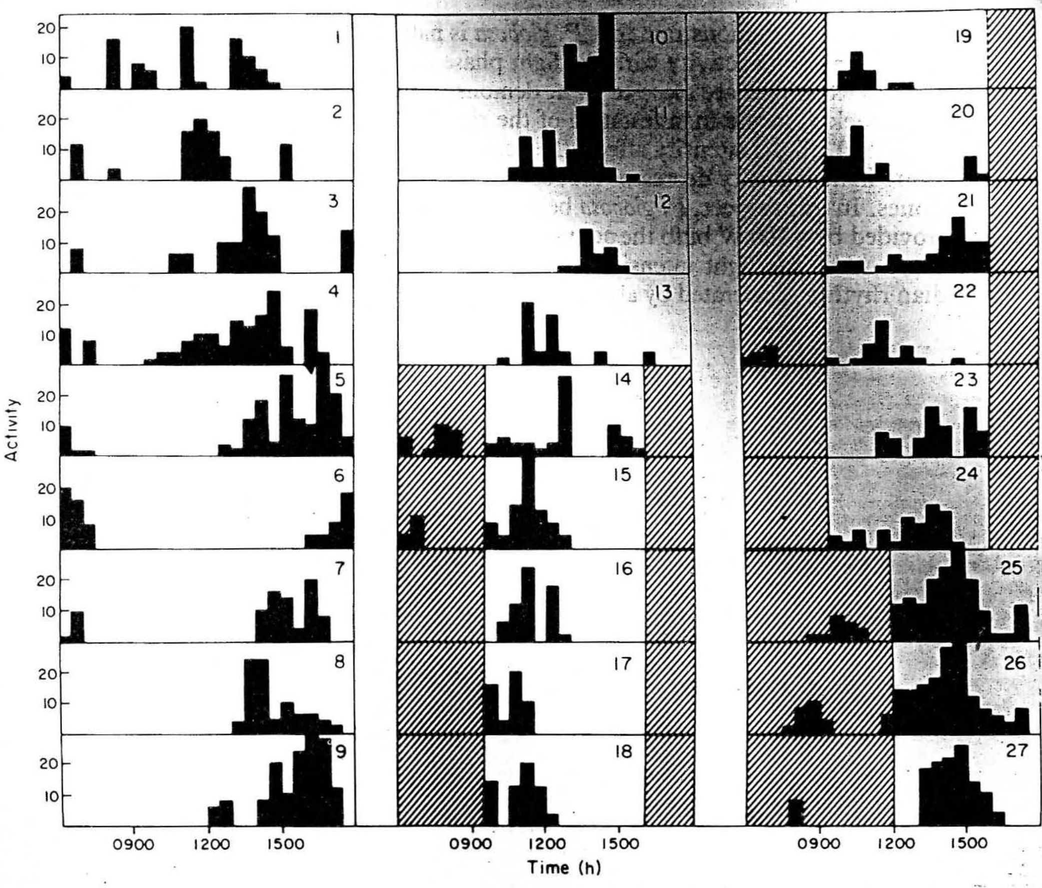

Figure 3. Activity record of an individual beetle free-running in LL (days 1–5, 100 W tungsten bulb) (days 6–13, 40 W bulb). Entrainment to LD 17·5: 6·5 (days 14–24, 40 W bulb) and LD 12:12 (days 25–27, 40 W bulb). Hatching indicates darkness.

17·5 h darkness (LD 6·5: 17·5), to LD 12:12, or to LL (constant light). Phase shifts were produced by advancing the LD cycle relative to the previous LD cycle. Light was provided by either 40 or 100 W tungsten bulbs suspended 60 cm above the activity cages. The temperature was maintained at 15°C (±1°C range). The numbers of pen deflections on the event recorder produced during each hour were analysed in the form of histograms, and each day's activity record was plotted below that of the preceding day (Fig. 3).

Results

In LD, the beetles were day-active, with locomotion beginning after the onset of light and ending at the light–dark transition (Fig. 3). In LL (100 W bulb) the activity rhythm free-ran with a period length longer than 24 h (Fig. 3, days 1–5). When the light intensity was reduced by about half (40 W), on day 6, the frequency of the circadian activity rhythm increased and, for the subsequent 5 days, it free-ran with a period of less than 24 h (Fig. 3, days 6–13). Finally, entrainment occurred at the onset of light in LD 17·5: 6·5 (Fig. 3, days 14–24) and LD 12:12 (Fig. 3, days 25–27).

Conclusions

These experiments demonstrate that *P. globosa* is naturally day-active. The external LD cycle synchronises its activity with the light phase of the cycle. In LL, the activity free-runs with periods that are close to 24 h, demonstrating the involvement of endogenous circadian clock(s) in the manifestation of the rhythm. According to the 'circadian rule' (Aschoff, 1961), light intensity affects the period of the free-running rhythm of animals. Increasing light intensity decreases that of day-active animals and accelerates it in night-active ones. In this respect, *P. globosa* behaved in LL as a day-active animal. When light was provided by a 100 W bulb the activity rhythm free-ran with a period that was longer than 24 h; when the light intensity was decreased by more than half (40 W bulb) the circadian rhythm accelerated by about 2–4 h (Fig. 3).