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Circadian activity rhythms in colonies of 'blind' molerats, *Cryptomys damarensis* (Bathyergidae)

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Various activity rhythms (general, feeding, and toilet) were measured under controlled laboratory conditions in two colonies of the Damara molerat *Cryptomys damarensis*, for 140 consecutive days (following a 30 day test period) under various photoperiod regimes (16 : 8 LD, 12 : 12 LD, and constant dark DD). As a general rule, all activities showed a significant diurnal rhythm with a period of 24 h under LD photoperiods. However, under a 16 : 8 LD photoperiod a very prominent activity component during the first part of the subjective night was observed, especially following a shift in photoperiod. The molerats responded rapidly to LD phase shifts. In constant dark, all activities had free-running periods of τ = 24,1–24,2 h, thus indicating that light can synchronize and entrain endogenous circadian rhythms in these molerats.

Verskeie aktiwiteitsritmes (algemeen, voeding en toilet) is onder gekontroleerde laboratoriumtoestande gemeet in twee kolonies van die Damara vaalmol *Cryptomys damarensis*, vir 140 agtereenvolgende dae (na 'n 30 dae toetsperiode) onder verskeie fotoperiodes (16 : 8 LD, 12 : 12 LD, en ononderbroke donker DD). Oor die algemeen het al die aktiwiteite 'n betekenisvolle daaglikse ritme met 'n periode van 24 h onder LD fotoperiodes getoon. Daar was egter gedurende die 16 : 8 LD fotoperiode 'n baie prominente aktiwiteitskomponent tydens die eerste deel van die subjektiewe nag, veral na 'n verandering in fotoperiode. Vaalmolle het baie vinnig op die LD faseveranderings gereageer. In ononderbroke donker het alle aktiwiteite aaneenlopende periodes van τ = 24,1–24,2 h gehad, wat aandui dat lig interne sirkadiese ritmes in hierdie vaalmolle kan meebring en sinkroniseer.

The five genera of subterranean rodents of the family Bathyergidae (Rodentia), known as molerats, are restricted to Africa south of the Sahara Desert (Nevo 1979; De Graaff 1981). Molerats spend their entire lives underground in sealed burrow systems, and very seldom venture above ground. Two genera, *Heterocephalus* and *Cryptomys*, are of particular scientific interest since they are the only eusocial mammals known to date (Jarvis 1981; Bennett & Jarvis 1988b).

Despite recent increased attention to bathyergid ecophysiology, one important aspect which has received no attention concerns their photo-responsiveness. Since Eloff (1958) reported that the structurally and functionally degenerated eyes of *Cryptomys* and *Bathyergus* are 'insensitive to light', some molerat studies have assumed (Lovegrove 1986; Lovegrove 1988) a lack of marked circadian rhythms of, for instance, activity, body temperature, and metabolic rate, which have been observed in other animals (see Aschoff 1970).

All bathyergids have very small vestigial eyes (Figure 1) which are generally kept closed when active, but which are characteristically opened when the molerat is alarmed (Eloff 1958, pers. obs). It has therefore been assumed that molerats are essentially blind, with the vestigial eye limited to possible alternative functions such as the detection of wind currents in the burrow (Eloff 1958).

Nevertheless, most bathyergids show clear circannual responses particularly the sub-tropical species. *Bathyergus, Georychus* and *Cryptomys* have distinct breeding seasons (Jarvis 1969; Van der Horst 1970; Taylor, Jarvis, Crowe & Davies 1985; Bennett & Jarvis 1988a), compared with the tropical species, *Heterocephalus glaber*, which breeds throughout the year (Jarvis 1981). Moreover, *Cryptomys damarensis* and *Cryptomys hottentotus* also show seasonal moult patterns (Nigel Bennett pers. comm.).

If some bathyergids display circannual rhythms, then we should expect these species to display certain circadian rhythms which measure day-length and thus enable the molerats to respond reproductively to seasonal change (see Elliot & Goldman 1981). What then, is/are the *zeitgeber* to

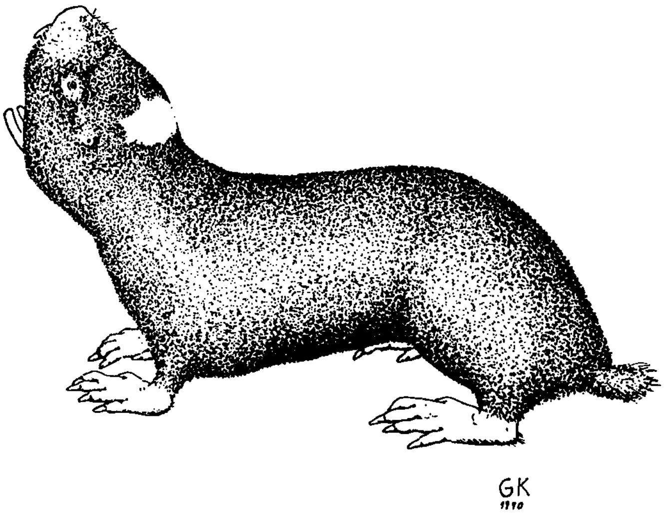

Figure 1 Drawing of a *Cryptomys damarensis* showing the location of the *bles* — the patch of white fur on top of the head, and the characteristic pose of the molerat when alarmed (when the small vestigial eyes are kept open). Drawing by Gerhard Körtner.

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which the Bathyergidae respond and thereby keep track of seasonality?

This question has received very little attention. Bennett, Jarvis & Davies (1988) have suggested that latitudinal differences in seasonal burrow temperatures could be the most important cue for seasonal reproductive and thermoregulatory preparedness. Indeed, when compared with the relatively constant seasonal burrow temperatures of tropical subterranean habitats (Brett 1986), the sub-tropical habitats show marked and predictable circannual burrow temperature fluctuations (Bennett *et al.* 1988; Lovegrove & Knight-Eloff 1988).

In this paper, we conduct the first investigations of the rhythms of the Bathyergidae in terms of photo-responsiveness under controlled conditions, using two colonies of the eusocial species *Cryptomys damarensis*. Our minimum objectives were to establish whether (i) *C. damarensis* display daily activity rhythms, (ii) if so, how they entrain these rhythms to specific photoperiods, (iii) whether, or how, they respond to photoperiod phase shifts, and (iv) whether they display a free-running activity rhythm under conditions of constant darkness.

In short, these objectives attempted to establish whether *C. damarensis* display characteristics of the circadian pacemaker model(s) developed from the data for other small nocturnal rodents (e.g. Pittendrigh & Daan 1976a, 1976b, 1976c). These model(s) are based on the observation that in all rodents investigated to date, endogenous oscillations believed to be generated in the suprachiasmic nucleus (Menacker, Takahashi & Eskin 1978; Rusak & Zucker 1979) are responsive to photoperiod in a pattern orchestrated by melatonin release from the pineal gland (Reiter 1980), thereby generating coupled locomotory activity patterns entrained to light/dark regimes.

The following abbreviations are used in this paper: LD light-dark photoperiod; DD constant dark; LL constant light; ρ rest time fraction; α activity time fraction; τ period (hours) of free-running (DD) circadian rhythm; NAC night activity component; DAC day activity component; SCN suprachiasmic nucleus.

Materials and Methods

The molerats used in this study were part of 15 molerats that were trapped in the Kalahari Gemsbok National Park, South Africa, in February 1989. Two incomplete colonies of *C. damarensis* (i.e. not all molerats in the natural colony were trapped) were ultimately used in this study. Colony A had five individuals, three males (109 g, 131 g, and 175 g), and two females (125 g and 131 g), whereas Colony B had four individuals, three males (133 g, 165 g, and 184 g) and one female (125 g). All molerats were transported from the Kalahari Desert by road to Cape Town for veterinary inspection, and then flown to Germany in late February 1989.

In Marburg, the two colonies were housed in simulated burrow systems each containing three rectangular plastic chambers (6,16 l) interconnected to one larger, common chamber (13,68 l), with glass-covered PVC guttering acting as 'burrows' (Figure 2). Once the molerats became accustomed to the burrow system, they chose each of the smaller chambers for specific functions as a nest chamber, a food-storage chamber, and a toilet chamber. The particular function of these chambers was retained by the molerats throughout the experimental period. Untreated sawdust was placed in the common chamber when the burrow system was cleaned every week.

The molerats were fed a diet of chopped apples, carrots, sweet potato, and potato, and were maintained on a 16 : 8 LD photoperiod at an ambient temperature of 28–30°C for three months prior to the activity measurements.

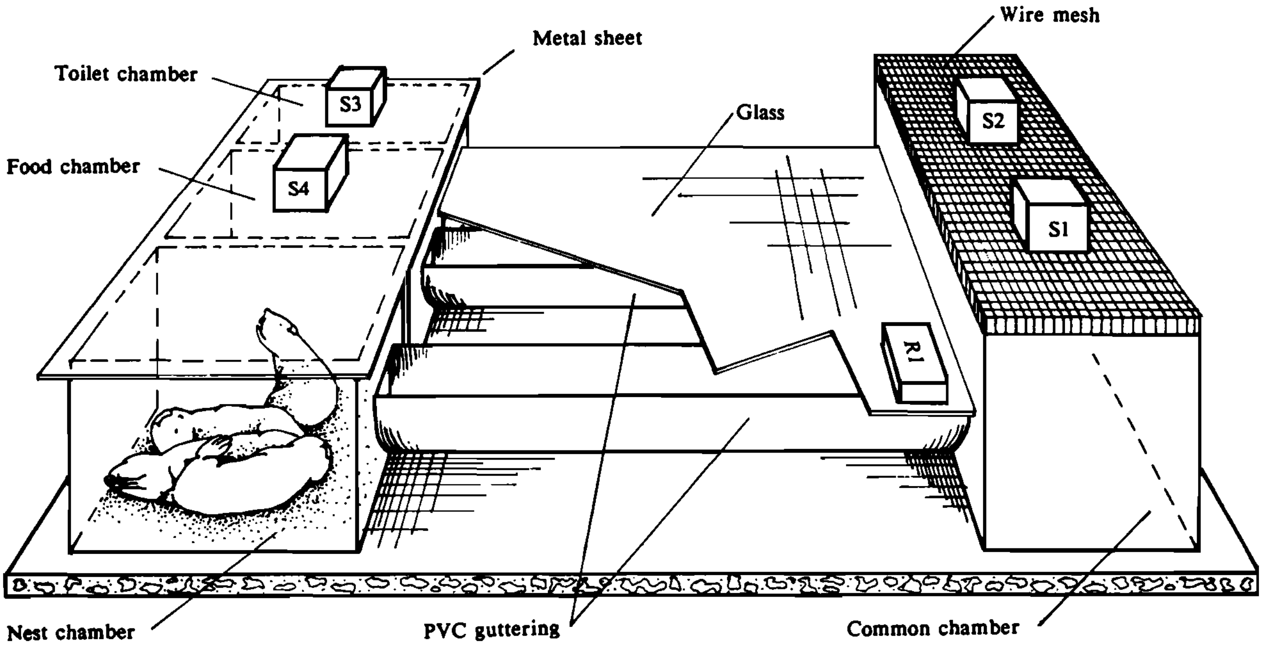

Figure 2 Schematic diagram of the simulated burrow systems in which *C. damarensis* were housed, showing the location of activity sensors S1–S4. The sensors situated over the common chamber were each positioned over a rectangular hole cut into the metal sheet covering the chamber. R1 is a radio reciever used and referenced in an associated study. Not to scale.

The study was conducted in a climate room with a light intensity of 200 lx at a constant temperature of 28,2–29,0°C. Although the climate room was fitted with cold-lights, the temperature in the room was measured (0,1°C) and plotted on a calibrated chart recorder for three days to establish the thermal characteristics of the room, particularly at the important lights-on and lights-off times. Lights-on and lights-off caused maximum 0,8°C increases and decreases in room temperature at the rate of *ca.* 0,3°C.h^{-1}.

Activity was measured every 6 min by summing the number of times passive infra-red activity sensors (S1–S4) situated in various parts of the burrow system (Figure 2) were activated by molerats moving within the detection range of the sensors. All movements detected by the sensors were registered as single events by a 2 s voltage output signal from the sensors. The positions of the sensors were chosen so that the molerats would have to pass underneath all sensors in order to enter or leave any of the chambers. All sensors were interfaced with a microcomputer.

To test our design, we initially set up this experiment using a single activity sensor (S1) and measured activity for 30 consecutive days. The choice of 16 : 8 LD photoperiod at that time was actually intended to simulate summer conditions for an associated study. However, since these preliminary data seemed so curious and so different between the two colonies (Figures 4 and 5), we decided to expand the study by incorporating additional sensors to quantify specific activities, and to switch to a 12 : 12 LD photoperiod so that our data could be interpreted in terms of standard circadian models. In this later study we measured activity for 140 consecutive days — these data are presented in Figures 6–9.

The molerats were fed every two days at non-specific times during natural daylight hours for all LD photoperiods, and during natural night hours during DD. Mostly, this could be done by quietly entering the room and placing food in the food chamber without alerting the molerats to human presence. The only obvious major disturbance that the molerats endured was during the 5–10 min required to clean the burrow systems once per week.

During all photoperiods the room was fitted with a white-noise generator, and during the constant dark period, a dim red light was kept on at all times.

Activity measures were double-plotted to facilitate an easier visual representation of circadian rhythms. Chi-square periodogram analyses (Sokolove & Bushell 1978) were used to test for significant ($p < 0{,}01$) circadian activity rhythms. These were calculated from the last 20 days of each photoperiod regime. Under DD and all photoperiods, the period with the highest QP value calculated by the chi-square periodogram analysis was taken as the period length under that light regime.

Results

Under LD photoperiods, both colonies showed significant ($p < 0{,}01$) 24 h activity rhythms in all activities with the exception of toilet activity in Colony A (Figure 3). Acto-

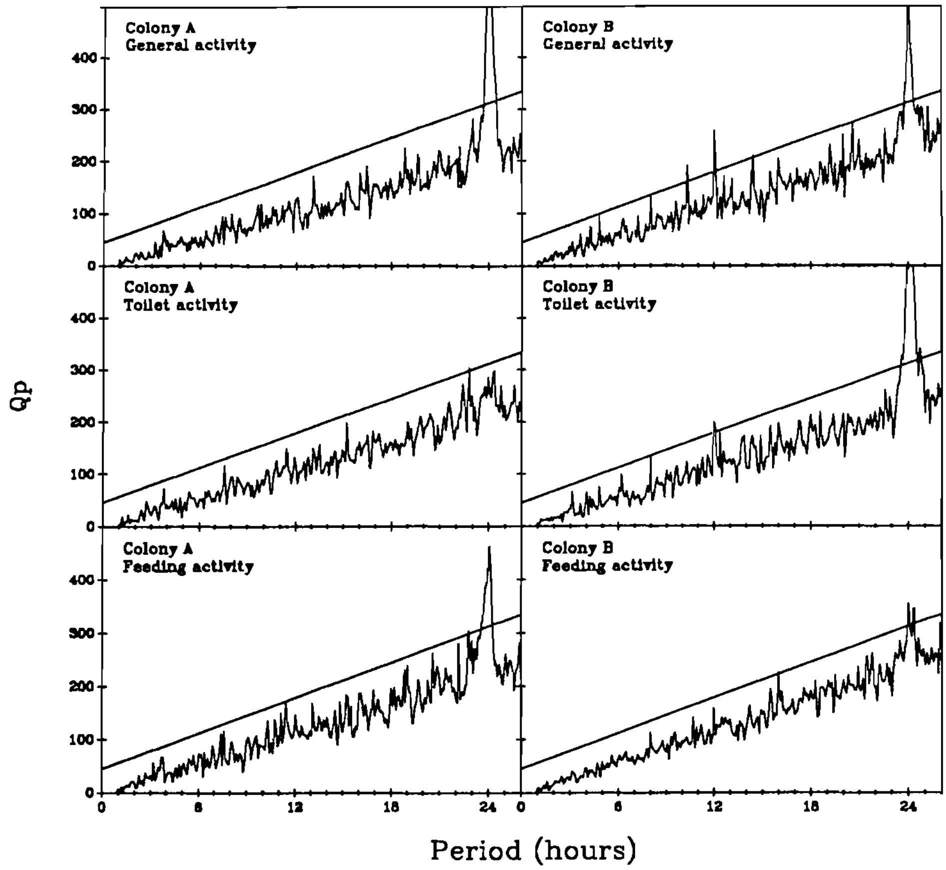

Figure 3 Periodogram analyses of the last 20 days of all three activities of both colonies as described by Sokolove & Bushell (1978). The straight line is drawn through critical values of χ^2_{p-1} for $\alpha = 0{,}001$ (approximately the 0,01 significance level) calculated from Zar (1984).

grams are presented here for the general activity of both colonies during the initial 16 : 8 LD photoperiod (Figures 4 & 5), the general activity of both colonies (Figures 6 and 7), the toilet activity of Colony B (Figure 8), and the feeding activity of Colony A (Figure 9) during the multi-photoperiod study.

As a general rule, activity measures were clearly higher during the subjective day. These patterns were strongest in the general activity patterns and weakest in the toilet activity of Colony A and the feeding activity of Colony B (Figure 3).

During the last 20 days of DD, both colonies had significant free-running circadian rhythms in all three activities with the exception of feeding activity in Colony B (Table 1). The periods of these rhythms (τ) all exceeded 24,0 h, ranging between τ = 24,1–24,2 h (Table 1).

However, one unexpected observation in this study was that, in addition to the underlying diurnal pattern, Colony B

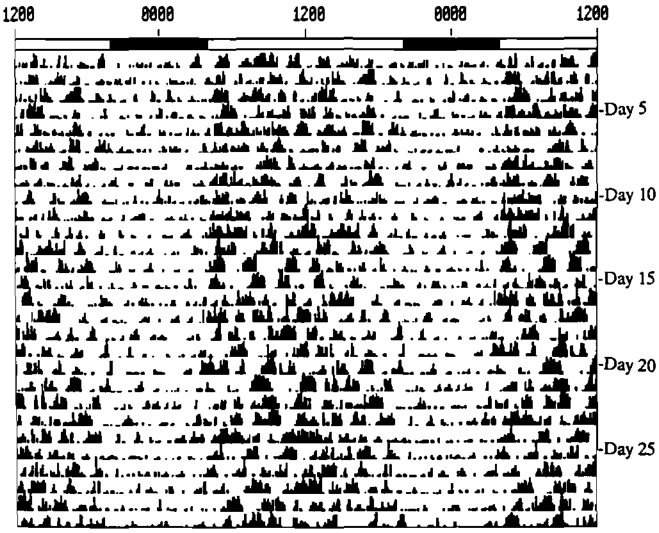

Figure 4 Actogram of general activity of Colony A during the initial test 16 : 8 LD photoperiod. As in all subsequent figures, the solid bars (dark hours) and blank bars (light hours) indicate the photoperiod(s) used. Data are double-plotted for easy visualisation of circadian rhythms.

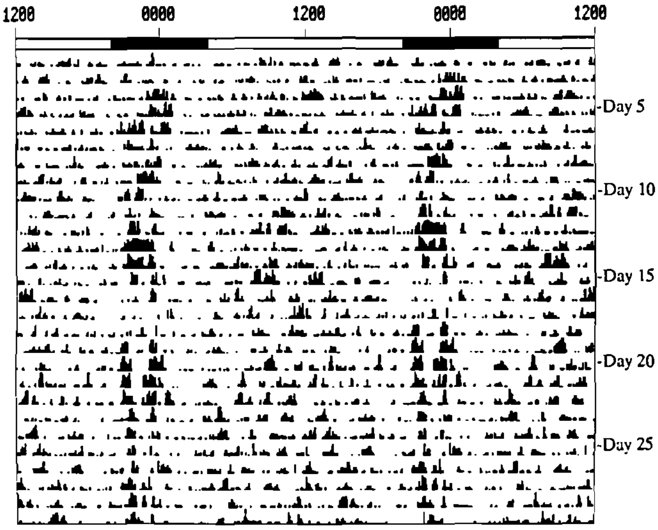

Figure 5 Actogram of general activity of Colony B during the initial test LD 16 : 8 photoperiod.

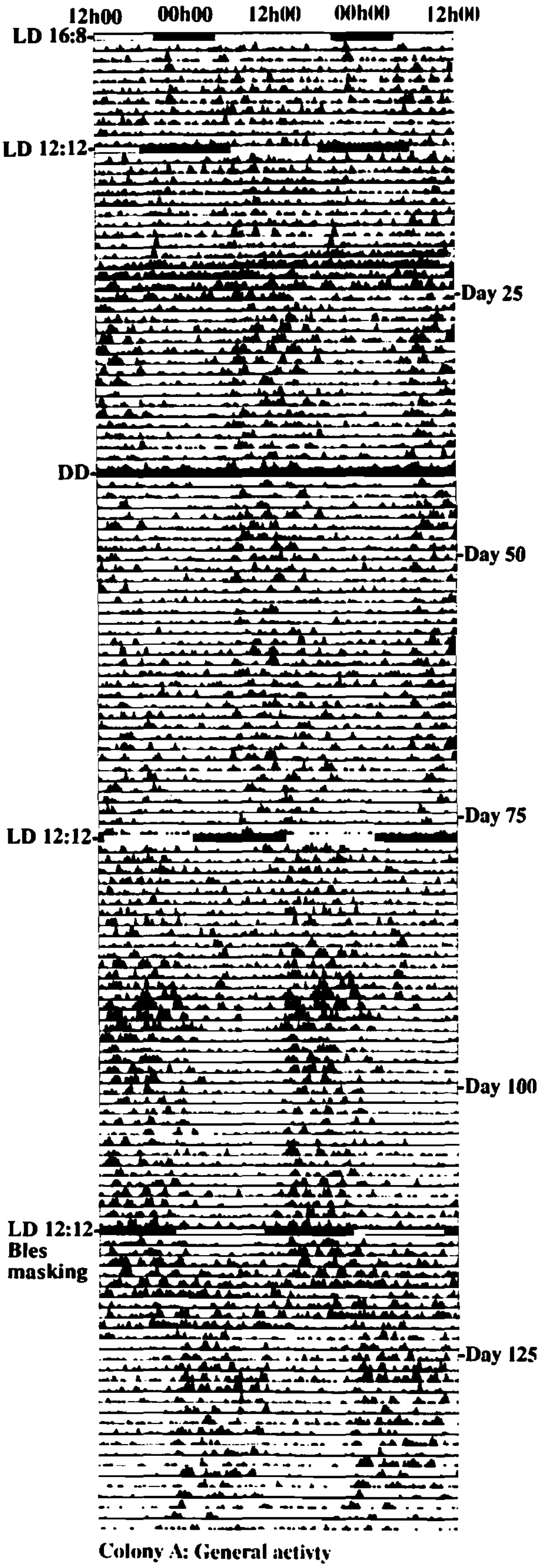

Figure 6 Actogram of the general activity of Colony A (Sensor 1).

displayed a very prominent activity component during the first half of the night under 16 : 8 LD photoperiods (Figures 5 & 7). This pattern was very clear and persisted for about 50 days before disappearing during the onset of the 12 : 12 LD photoperiod of the expanded study (Figure 7). For clarity, we henceforth refer to this as the night activity compo-

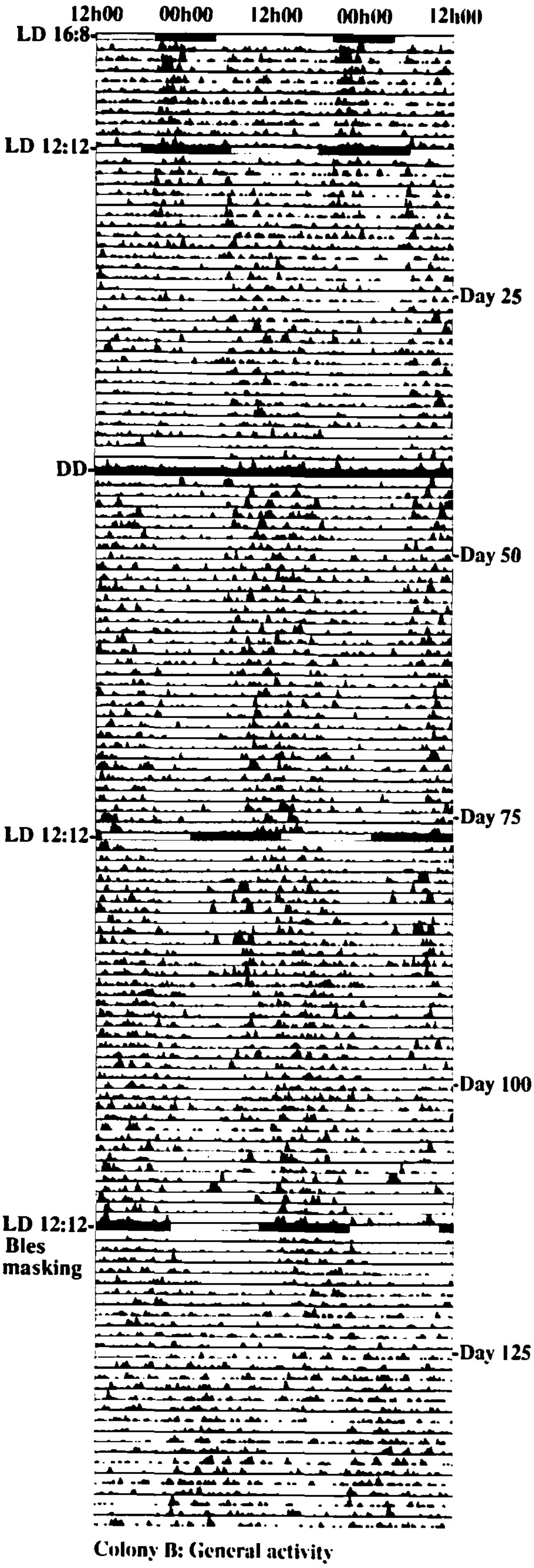

Figure 7 Actogram of the general activity of Colony B (Sensor 1).

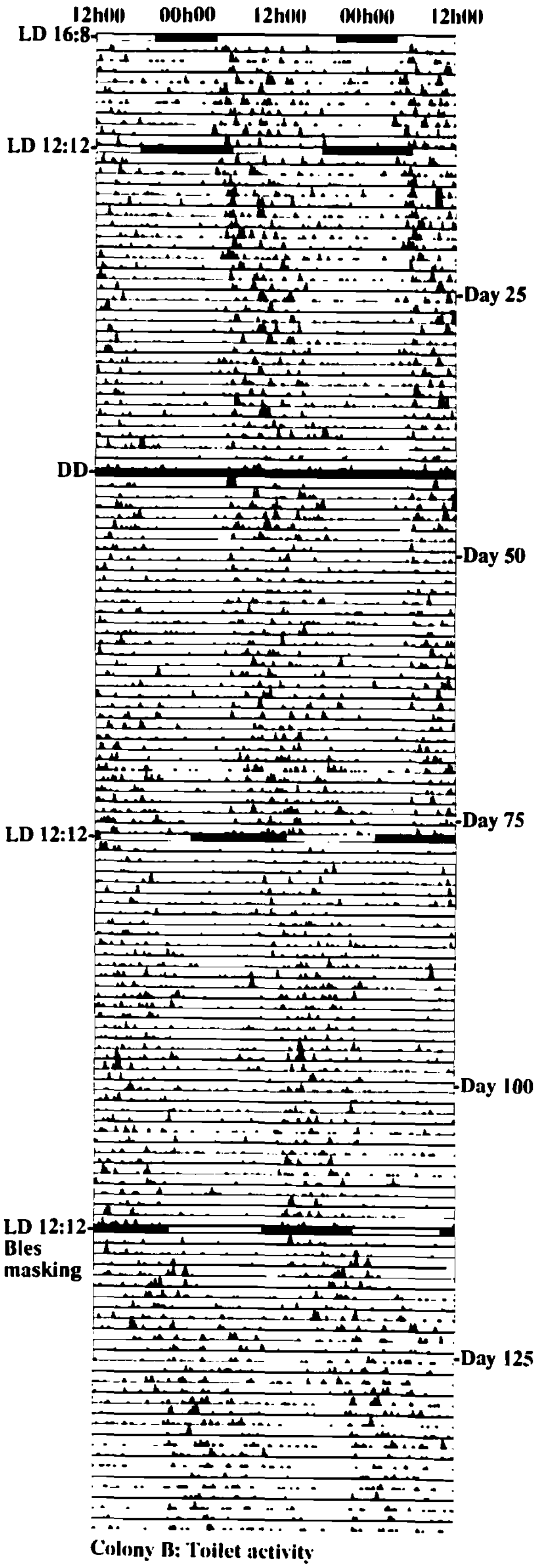

Figure 8 Actogram of the toilet activity of Colony B.

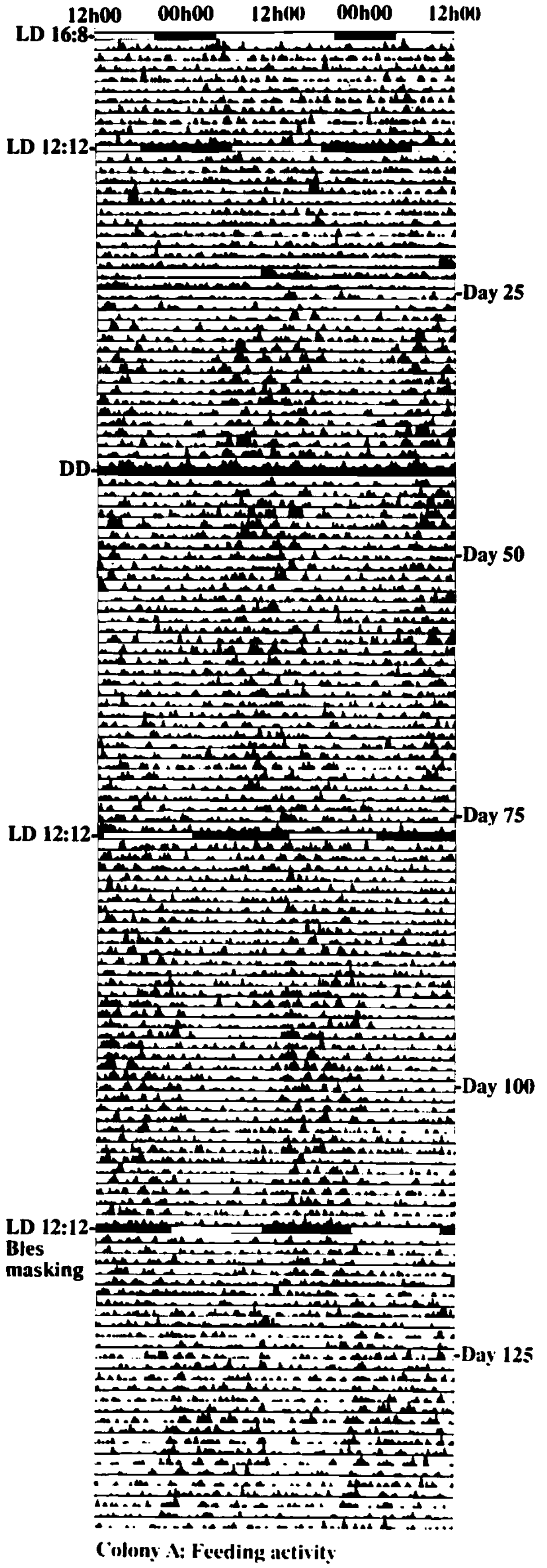

Figure 9 Actogram of the feeding activity of Colony A.

Table 1 Free-running periods of activities (τ) during the last 20 days in constant dark (days 59–79) calculated using chi-square periodogram analyses (Sokolove & Bushell 1978, see Figure 3 legend). NS = not significant

		Colony A		Colony B	
Activity	Sensor	p	τ (hours)	p	τ (hours)
General	S1	< 0,01	24,1	< 0,01	24,2
General	S2	< 0,01	24,2	< 0,01	24,2
Toilet	S3	< 0,01	24,1	< 0,01	24,2
Feeding	S4	< 0,01	24,2	> 0,01	NS

nent (NAC), and to the day activity as the day activity component (DAC). In Colony B, the gradual weakening of the NAC in 12 : 12 LD seemed to be accompanied by a corresponding strengthening of the DAC (Figure 7). In both colonies the NAC, although not as strong as during the 16 : 8 LD, appeared again a few days after the start of the phase-shifted 12 : 12 LD following DD (Figures 6 & 7). Colony A also showed the same evidence of this NAC during the 16 : 8 LD of the multi-activity study (Figure 6). However, the toilet and feeding activities of both colonies clearly lacked any evidence of the NAC under all photoperiods (Figures 8 & 9).

In 16 : 8 LD, the NAC onset was *ca.* 1 h after the onset of dark, and had a duration of *ca.* 3 h. In Colony B, the mean activity values during the NAC were *ca.* 2–3 times higher than those recorded during the day, and *ca.* 8–10 times higher than the activity recorded during other times during the night (Figure 5).

In both instances where phase shifts were made to the photoperiod, i.e. the two photoperiods following DD, the onset of the diurnal activity entrained fairly rapidly to the new photoperiod (Figures 6–9).

Discussion

There is no doubt that *C. damarensis* can perceive light and synchronize their activity patterns to a photoperiod. The best evidence of this was the free-running period exceeding 24 h when light cues were removed under conditions of constant darkness. When the night activity component was not present, the molerats responded to specific photoperiods by maintaining the duration of their activity (α) and rest (ρ) fractions proportional to the time durations of the light and dark phases, respectively. This suggests that the small increments in room temperature associated with lights-on was unlikely to be the *zeitgeber* to which the molerats entrained activity onset in this study.

Moreover, the colonies also clearly responded to photoperiod phase-shifts similar to those observed in spalacid molerats (Rado, Gev & Terkel 1988) and other rodents (Pittendrigh & Daan 1976a, 1976b, 1976c). However, the NAC was a circadian pattern which, as far as we are aware, has not been observed in rodents before. Consequently, when it was expressed (e.g. Figure 5) it was not immediately obvious which light/dark phase represented the α and ρ components categorizing diurnal and nocturnal species (Pittendrigh & Daan 1976a, Elliot & Goldman 1981). However, since both colonies consistently showed the strongest entrainment of all activities to the onset of light, it is reasonable to conclude that *C. damarensis* is essentially a diurnal species.

Since we cannot define the influence of social entrainment, we must restrict our conclusion to the observation that the colony as a whole displays patterns of entrainment of activity to particular photoperiods, which are synonymous with the patterns of entrainment of activity oscillators seen in solitary, individual diurnal rodents.

Both colonies showed a free-running activity pattern in the absence of a light *zeitgeber*. But again, because of the possible role of social entrainment, this need not necessarily imply that all individuals had $\tau > 24$ h. Since intra-specific variation in τ is common (Pittendrigh & Daan 1976a), the observation that α and ρ maintained their period lengths or did not tend towards aperiodism in DD implies that social entrainment did occur. The idea here is that, if some molerats phase advanced ($\tau < 24$ h), and some phase delayed ($\tau > 24$ h), the α and ρ patterns should dissolve into a pattern lacking any clear photoperiodism. In fact, the social structure of *C. damarensis* colonies should intrinsically maintain intra-colony τ variation. Firstly, *C. damarensis* display age-dependent differentiation of labour in which the younger molerats do most of the work e.g. burrowing (Bennett & Jarvis 1988b). Intense locomotory activity can markedly increase the rate of re-entrainment to shifted photoperiods, and may even have a modifying feedback influence on the frequency of the pacemaker clock itself (Mrosovsky & Salmon 1987). Secondly, the age structure of the colony must be considered since τ changes with age — decreases in the case of nocturnal rodents (Pittendrigh & Daan 1976a).

A functional role for the NAC?

The night activity component was one of the intriguing observations made in this study, so let us pursue a few possible explanations in terms of the pacemaker models. Aschoff (1954, 1957) and Pittendrigh & Daan (1976c) have suggested that activity patterns displayed by nocturnal rodents could be represented by two coupled, SCN-generated oscillations, one a 'morning' oscillator, and the other an 'evening' oscillator. These two oscillations, they argue, produce the characteristic 'two-peak' activity patterns seen in nocturnal rodents.

The first option is that the NAC could represent a form of the 'splitting phenomenon' of the evening and morning oscillations of α, such as has been observed in nocturnal rodents under high light intensity LL (Pittendrigh & Daan 1976c). However, in this study the NAC maintained a period of 24 h when present under LD and did not show any tendency towards either merging, or splitting with the main activity component — two characteristics of α-splitting.

The second option is that the NAC disappeared in response to a shortening of the photoperiod (16 : 8 LD to 12 : 12 LD). In other words, the NAC may be masked by photoperiods less than some critical photoperiod and may thus only be expressed under certain photoperiods. In this respect, the NAC may also represent an artifact of the circadian system induced by unnatural photoperiods under which these animals did not evolve — in this case, unnaturally long days.

Another alternative is that these molerats may possess two activity oscillators, which, instead of being entrained to the beginning and the end of the α phase as described above for nocturnal rodents, may represent daytime and nighttime oscillators. In other words, one oscillator is entrained to the onset of light, and the other to the onset of dark. However, before we extend this idea, we need to discuss the type of locomotion which occurred during the NAC and which can account for the more intense activities measured during this part of the night.

Although it was not possible to observe directly the activity of the molerats during the NAC, from various observations it can reasonably be concluded that this activity phase can be considered equivalent to bouts of maximum burrowing activity such as might occur in free-ranging molerats. These activity bouts were only recorded in the wire-mesh-covered common chamber; the only region of the burrow system that was not covered by glass or metal, and which was therefore exposed to the room environment. From behavioural observations made prior to the start of activity measurements, it was noted that both colonies treated this common chamber as the 'area of danger', or, the 'above-ground region' of the burrow system. Apart from 'mound building' and 'sweeping activity', involving pushing and kicking the sawdust into the common chamber, and 'excavating' activity, involving intense gnawing of the PVC tubing at the entrance of each burrow (burrowing activities typical of this species; Lovegrove 1989), the common chamber was seldom occupied. When moving from one chamber to another, the molerats tended to dash from one burrow entrance in the common chamber to another.

The second point is that when the NAC was present, the intensity of activity recorded was always greater during the NAC than during any other time of the day. Such intense activity could be registered either by (i) intense activity at a stationary position in the common chamber, such as might occur during gnawing, or (ii) rapid and repeated movement in and out of the common chamber, such as occurs during sweeping and mound-building behaviour (see Lovegrove 1989).

In an associated circadian metabolic study, Lovegrove & Heldmaier (unpubl. data) found that although there was generally no marked circadian body temperature rhythm in *C. damarensis* during the initial 16 : 8 LD study, one individual showed significant daily maximum increases in body temperature which corresponded precisely with its individual NAC. This observation suggests that the increased body temperatures during the NAC are a consequence of metabolic heat production generated by intense activity.

For the moment, our best suggestion is that the NAC represents a separate activity oscillator specific to burrowing behaviour and mole-hill construction, and which entrains to the first part of the night. The gradual disappearance of the NAC may reflect the novelty of a complex simulated burrow system, compared with the relative simplicity of a large glass aquarium in which the molerats were first housed during acclimation. This problem has been encountered in more routine running wheel activity studies using rodents, in which the novelty of having a running wheel wears off after intense initial wheel-running. In our case, the novelty involved the initially intense, gnawing, sweeping, and sawdust-kicking 'mole-hill construction' behaviour which clearly became less frequent as this lengthy study progressed. If our suggestion is correct, then this problem could be solved by presenting the molerats with a mechanical burrowing mechanism simulating a soil burrow-face.

There are encouraging analogies to the NAC in the form of intense free-ranging burrowing activity extended 2–4 h into the early night in a solitary bathyergid (Jarvis 1973), in *C. damarensis* (Lovegrove 1988), in spalacid molerats (Rado & Terkel 1989), and in geomyid pocket gophers (Gettinger 1984). Interestingly, however, in a laboratory study under controlled conditions, Rado *et al.* (1988) found no evidence of a NAC in *S. ehrenbergi*. But again, this may be simply because the molerats were denied the opportunity of burrowing under the experimental conditions concerned. In their natural habitat, *S. ehrenbergi* (Rado & Terkel 1989) and *Heliophobius argentocinereus* (Jarvis 1973) also delayed the onset of their diurnal activity to 2–4 h after the onset of the natural photoperiod.

In interpreting their trends, Rado & Terkel (1989) have suggested that although light remains the main *zeitgeber* in *S. ehrenbergi* (Rado *et al.* 1988), these molerats 'fine-tune' their activity rhythm to include a major digging activity component in the early night when burrow temperatures reach a maximum. Together with their data, this interpretation implies that a single oscillator, although entrained by light, can be shifted 2–4 h out of phase with the natural photoperiod in response to natural soil temperature oscillations.

In developing a common, future working hypothesis, it may prove worthwhile merging this latter interpretation with our two-component DAC-NAC hypothesis. For instance, we need to establish whether the NAC is expressed independent of temperature *zeitgeber* or activity feedback, whether individuals kept in isolation show free-running phase-relation splitting of α from NAC (or *vice versa*) under constant conditions (LL), and importantly, what the possible functional significance of the NAC may be in terms of free-ranging entrainment to natural photoperiods.

This latter issue also requires an appreciation of the influence or effects of free-ranging social entrainment. The synchronization of individual τ's may be important in terms of nest-huddling and the thermoregulatory benefits thereof (Withers & Jarvis 1980). Assuming for the moment, that intracolony τ does exist, social entrainment should prevent aperiodic patterns of colony activity, or decrease the rate at which the natural free-running activity rhythm drifts out of phase with the natural photoperiod. In this latter respect, a colony τ not much greater than 24 h is advantageous, since α will, as we have observed, drift slowly out of phase with the natural photoperiod and re-entrain fairly rapidly to a new light *zeitgeber*.

At this stage we do not know what the colony τ represents. It could represents the τ of a single animal, possibly that of the dominant male in the colony (see Bennett & Jarvis 1988b), to which the colony entrains its activity rhythm. If so, this animal could be considered to be the 'colony clock', and would be the only individual which theoretically would require a regular light *zeitgeber*.

Although molerats live and forage underground permanently, unlike the American pocket gophers which may feed on the surface from the relative safety of 'popholes', they should theoretically be exposed to light, maybe only momentarily, every time that they are close to, or break the soil surface to construct mole-hills. However, mole-hill construction by *C. damarensis* is dependent on season and the soil-moisture content of the sand (Lovegrove & Painting 1987; Lovegrove 1989), and may not be that regular. For instance, during a field study of a complete colony of 22 *C. damarensis* in the Kalahari Desert (Lovegrove 1988), it was observed that for a period of at least one month, not one individual in the colony broke the soil surface. This observation suggests that, at least at certain times of the year, e.g. during the dry season (see Lovegrove & Painting 1987), colonies of free-ranging *C. damarensis* may not receive light pulse *zeitgebers* for extended periods of time.

If we accept the NAC as the circadian time during which our assumed colony-clock-individual (with its own 24,1 h < τ < 24,2 h) has the greatest probability of recieving a *zeitgeber*, this may only occur after 15–30 days of natural DD — the time required for the end of the NAC to drift towards, and coincide with the onset of the next natural day. Regular *zeitgeber* may therefore be less important to *C. damarensis* than, for instance, to other solitary nocturnal rodents where inappropriate activity timing may be fatal. This is especially true if factors such as soil and burrow temperature fluctuations are not important to the molerats in terms of foraging. Moreover, a reduction in the incidence of mole-hill construction should lower the probability of predator invasion of the burrow system.

It seems clear that the above speculation calls for the development of appropriate models which integrate intracolony chronobiological statistics, such as τ variation and the characteristics of phase response curves (see Pittendrigh & Daan 1976b), with behavioural data, such as intra-colony dominance and worker differentiation. This should be considered to be the minimum data required to explain how colonies of *C. damarensis* may keep track of seasonal daylength.

A pineal third eye in molerats?

During the last 30 days of this study, we attempted to test the hypothesis that the *bles* may act as a 'photon window' permitting direct light stimulation of the pineal gland. The *bles* is a patch of white hair found on the heads of most bathyergids (Figure 1), directly overlying the pineal gland. Author BGL has measured the light transmittance through this white fur relative to the surrounding hair, and has found it to be about 50–100 times higher. Quite simply, we masked the *bleses* on all animals using a patch of quick-setting epoxy resin dyed black with Indian ink.

Unfortunately, the *bles* patches either fell off, or were removed by the molerats, after various time periods following a phase shift in the photoperiod at the onset of this *bles* experiment. All patches were off after 12 days. This was a pity because some activities seemed to show fairly aperiodic patterns (Figure 6) or possible splitting of the activity component (6–9). We believe this experiment is worth repeating, but in retrospect we would use solitary bathyergids, e.g. *Georychus capensis*, and use an improved, more permanent method of light-proofing the *bles*.

Conclusions

In terms of the minimum objectives of this study, it can be concluded that *C. damarensis*, and therefore possibly all Bathyergidae, are photo-sensitive, possess a circadian system, and can entrain endogenous activity oscillators to particular photoperiod regimes. Moreover, the activities of the colony as a whole display the characteristic rodent free-running activity rhythms in the absence of light *zeitgeber*, with the lack of aperiodic patterns possibly being indicative of social entrainment.

The above observations invite much additional study of photo-perception in the Bathyergidae. For instance, the particular organ(s) or glands which could be most heavily involved in bathyergid light perception and melatonin synthesis e.g. the retina, harderian gland and pineal gland, remain completely unknown. In this respect the significance of the *bles* associated with possible direct pineal photo-sensitivity is an interesting prospect, since unlike *Spalax* in which the unusually large harderian gland is implicated (Balemans, Pevet, Legerstee & Nevo 1982; Pevet, Heth, Haim & Nevo 1984), *C. damarensis* has recently been found to have a very small harderian gland (S. Klaus pers. comm.). Of course, until direct experimental evidence is elucidated to the contrary, we must assume that the vestigial bathyergid eye is photo-sensitive (*cf.* Eloff 1958).

The existence of a night activity component superimposed on an underlying diurnal activity rhythm may represent a useful tool for further investigation of the two-component oscillation system and the expression of endogenous oscillators in subterranean rodents. In this respect, although future studies must include solitary bathyergids to overcome the complications of social entrainment, there is ample justification for pursuing a possible caste- and burrowing-related association with NAC expression.

Lastly, data on individual intracolony τ's are required before adequate hypotheses and models can be developed to explain how free-ranging *C. damarensis* may entrain to natural photoperiods, and how they are able to measure seasonal changes in natural daylength.

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