DAILY ACTIVITY OF FOUR TROPICAL INTERTIDAL HERMIT CRABS FROM SOUTHEASTERN BRAZIL

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(With 1 figure)

ABSTRACT

This study describes the daily activity in a simulated high tide situation of four species of hermit crabs (*Pagurus criniticornis*, *Clibanarius antillensis*, *C. sclopetarius,* and *C. vittatus*) that coexist in an intertidal flat in southeastern Brazil. Observations were done in two-hour intervals during two subsequent days (48 h) in three replicate pools with thirty crabs each. Among species (between and within genera) there was an evident variation in activity patterns, of which three could be distinguished. The circadian activity patterns of *C. antillensis* and *C. vittatus* could be characterized as evening and nocturnal, with resting peaks during the morning and afternoon. The circadian activity pattern of *C. sclopetarius* was characterized by two marked peaks of inactivity, corresponding to dawn and evening, which could represent an intrinsic association with the semi-lunar tidal cycles of the study area. *Pagurus criniticornis* showed high activity not influenced by day/night conditions during the entire observed period. These activity pattern variations of the studied hermit crabs should be taken into account in designing further experiments. More precise and accurate interspecific behavioral comparisons among species could be achieved in nocturnal experiments, the high activity period of all species.

Key words: rhythms, activity patterns, behavior, *Clibanarius*, *Pagurus*, Diogenidae, Paguridae.

RESUMO

Atividade diária de quatro espécies tropicais entremarés de ermitões do Sudeste brasileiro

Este estudo descreve a atividade diária, sob condição simulada de maré alta, de quatro espécies de ermitões (*Pagurus criniticornis*, *Clibanarius antillensis*, *C. sclopetarius* and *C. vittatus*) que coexistem em uma planície lodosa entremarés na região Sudeste do Brasil. As observações foram efetuadas em intervalos de duas horas durante dois dias subseqüentes (48 h) em três piscinas contendo 30 indivíduos cada. Verificou-se evidente variação nos padrões de atividade entre as quatro espécies de ermitões estudadas (entre e dentro dos gêneros). Três padrões foram evidenciados. O padrão circadiano de atividade de *C. antillensis* e *C. vittatus* pode ser caracterizado como crepuscular e noturno, com períodos de inatividade durante a manhã e início da tarde. O padrão circadiano de atividade de *C. sclopetarius* apresentou dois picos marcantes de inatividade, correspondentes ao nascer e ao pôr-do-sol, o que pode representar associação intrínseca com os ciclos de marés semilunares da área de estudo. *Pagurus criniticornis* mostrou alta atividade durante todo o período de observação, não sendo influenciado pelas condições diúrnas-noturnas. A variação nos padrões de atividade observados para esses ermitões deverá ser utilizada no planejamento de experimentos futuros. Além disso, maior precisão em comparações comportamentais interespecíficas entre essas espécies poderá ser obtida no período noturno, quando todas as espécies estão ativas.

Palavras-chave: ritmos, padrões de atividade, comportamento, *Clibanarius*, *Pagurus*, Diogenidae, Paguridae.

INTRODUCTION

Most crustacean species are subjected to cyclic light/dark environments associated with day and night periods. Diurnal and semi-diurnal tides are also periodic events that profoundly influence intertidal species. In fact, as DeCoursey (1983) and Webb (1983) have pointed out, crustaceans have biological rhythms that match some of the cyclic variations of their environments. Behavioral periodicities may have tidal, diurnal, semi-lunar, lunar, and annual components although circadian and circatidal activity patterns are specially common to crustaceans (DeCoursey, 1983; Webb, 1983).

Hermit crabs are very abundant in coastal areas (Reese, 1969) and have elaborate reproductive and shell-related behaviors (see Hazlett, 1981 for a review). In addition, they present behavioral rhythms that may be influenced by cyclic environmental conditions. *Pagurus longicarpus* (Rebach, 1978, 1981), *Clibanarius vittatus* (Fotheringham, 1975), and *Diogenes nitidimanus* (Asakura & Kikuchi, 1984; Asakura, 1987) may have a seasonal vertical migratory behavior associated with drastic variation in water temperature in intertidal and shallow subtidal areas throughout the year. Intertidal hermit crabs may have patterns of dispersal and clustering associated with the tidal cycle (Snyder-Conn, 1980; Gherardi & Vannini, 1989; Gherardi *et al.*, 1989). They are generally inactive in clusters or in refuges during low and high tides and present high activity during flood and ebb tides when they disperse to foraging areas. Tides also dictate the frequency of tree climbing behavior in the terrestrial hermit crabs *Coenobita caviceps* and *C. rugosus* in mangroves (Barnes, 1997a). Activity in the terrestrial hermit crab *Coenobita clypeatus* is nocturnal and associated with lower temperature and higher air humidity at night (De Wilde, 1973). Other terrestrial hermit crabs show nocturnal activity peaks but also present low frequency of particular behaviors during daylight (Barnes, 1997b). Ball (1968) showed that the activity patterns of the intertidal hermit crabs *Pagurus samuelis* and *P. granosimanus* follow the normal day-night conditions but do not persist under constant illumination or darkness. The activity periods of eleven Caribbean intertidal and subtidal hermit crabs were examined under high tide conditions (Hazlett, 1966) and revealed patterns that varied on subsequent days and among and within genera. Similarly, Mitchell (1973) recorded opposed activity patterns for two coexisting populations of *Pagurus bernhardus* (daylight activity) and *P. prideauxi* (nocturnal activity). Underwater field observations using time-lapse cameras showed reduced mobility in *Paguristes oculatus* in the dark hours and main activity during daylight (Stachowitsch, 1979). Hermit crab activity is habitat related (Barnes, 1997b), i.e., the frequency of crab activity varies according to the constraints imposed by different habitats. Thus, it is important to investigate if coexisting hermit crab species have intrinsic activity patterns dictated by the tides. To do this, it must be determined if such individuals, even when submersed and free from tidal influence, still present a circatidal and even a circadian component in their activity pattern as has been shown for pagurid and diogenid hermit crabs by Hazlett (1966).

Four intertidal hermit crabs species (*Pagurus criniticornis*, *Clibanarius antillensis*, *C. sclopetarius*, and *C. vittatus*) coexist in the Araçá region, São Sebastião Channel, southeastern Brazil. The activity patterns of these species in nature are influenced by the tides (Turra & Leite, 2000; Turra *et al.*, 2000). *Clibanarius sclopetarius* and *C. antillensis,* whether exposed or in refuges, generally cluster during low tides. *Clibanarius vittatus* withdraws into its shell and remains exposed to the air on or under rocks, or buries itself in the mud: in addition, it may undergo both vertical and horizontal dispersion at flood tides (Turra *et al.*, 2000). *Pagurus criniticornis* is less tolerant to emersion than the three coexisting *Clibanarius* species (Turra & Denadai, 2001) and is active during low tides only in tidal pools; otherwise, individuals of this species are buried in the muddy substrate. All these species may display some degree of activity on cloudy days or at nocturnal low tides (A. Turra, unpublished data). This study aims to describe the daily activity in a simulated high-tide situation for these four intertidal hermit crabs and was designed to test the hypothesis that these species have intrinsic rhythms independent of tidal cycles.

MATERIAL AND METHODS

Individuals of *Pagurus criniticornis*, *Clibanarius antillensis*, *C. sclopetarius*, and *C. vittatus* were collected in the tidal flat of the Araçá region, São Sebastião Channel, São Paulo State, Brazil (23°49'S, 45°24'W). Despite these species, partitioned microhabitats in nature, they may occupy all available substrate types, from mud to fragmented rocky shore (Turra *et al.*, 2000). The experiments were conducted in the Marine Biology Center of Universidade de São Paulo (CEBIMar-USP). A total of ninety individuals of each species was observed in three plastic swimming pools (1.8 x 1.3 m) with circulating seawater, comprising three replicates with 30 individuals each. Despite this density value being superior to that recorded in the field for the studied species (see Turra *et al.*, 2000), the use of a smaller number of individuals in the experiment would have caused inaccuracy in the estimates of mean frequency of active crabs. Moreover, the effect of crowding on hermit crab behavior can be considered negligible after periods of adjustment (Hazlett, 1968), justifying the three-day acclimation period in tanks before the experiments. [Experimentation with single crabs was not considered since isolation has a persistent positive effect on crab aggressiveness and a negative one on locomotory behavior (Courchesne & Barlow, 1971).] The pools were located outdoors in a shady place, under wide treetop, for natural illumination without direct sunlight influence. This caused a small fluctuation in the water temperature during the experiment (27.4 ± 0.7°C). The bottom of the pools was filled with sediment from the collection site.

The individuals were observed at 2 h intervals for 48 h and the most conspicuous behaviors were described and recorded. The nocturnal observations were done using a red light in order to avoid influencing crab behavior (Hazlett, 1966). The activity patterns were classified according to Hazlett (1966). Each behavior frequency was calculated for each replicate (pool) and then averaged for each species throughout the time intervals.

Preliminary observations revealed that the most conspicuous behaviors displayed by these hermit crabs were: 1. locomotory; 2. reproductive; 3. agonistic; 4. feeding; 5. stopped in the sediment surface; 6. burying; 7. retracted into the shell. The locomotory behavior was identified when the crabs were continually moving in the sediment surface using ambulatory legs and/or chelipeds. Reproductive and agonistic behaviors were observed and characterized following the descriptions of Hazlett (1966) for both diogenid and pagurid hermit crabs. Movements of the chelipeds toward the mouth region characterized feeding. Some hermit crabs were active but stopped in the sediment surface as if in a 'stand by' mode without moving any appendage, as also described for *Paguristes oculatus* by Stachowitsch (1979). They could present any of the above-mentioned behaviors as long as they wish, thus enabling the classification of such individuals as active. Burying was characterized by inactive crabs with their shells partially or totally covered by sand. Other inactive individuals were completely retracted into their shells so that pereopods could not be seen through shell apertures. Hypotheses concerning the relationship between particular behaviors were tested using the Pearson correlation analysis (Zar, 1999).

RESULTS

Clibanarius antillensis was frequently recorded walking or stopped in the sediment surface. Locomotory behavior showed a positive relationship with feeding (Pearson correlation: $n = 24$, $r = 0.42$; $p = 0.039$), while 'standby' did not show any clear circadian pattern (Fig. 1). Some of the individuals of *C. antillensis* were completely retracted into their shells, with shell apertures positioned either up or downward. Burying was rare in this species and was generally associated with clusters of inactive individuals. Agonistic and reproductive behaviors were seldom recorded. The pattern of activity of *C. antillensis* could be characterized as evening and nocturnal, with subtle resting periods during the morning and afternoon (Fig. 1). This pattern was less evident on the second day of observation. No relationship could be established between the activity pattern of this species and the tidal cycle during the observation period.

The most conspicuous behaviors presented by *Clibanarius sclopetarius* and *C. vittatus* were: burying, locomotory, and feeding (Fig. 1). Feeding peaks were positively associated with locomotion peaks for *C. sclopetarius* ($n = 24$; $r = 0.52$; $p = 0.009$) and negatively for *C. vittatus* ($n = 24$; $r = –0.46$; $p = 0.024$). This means that feeding in *C. vittatus* is independent of locomotion frequency, i.e., the crabs displace for reasons other than foraging. Activity peaks of these two species were alternated with inactivity peaks evidenced by relatively high frequency of buried individuals. Clusters of inactive individuals were also recorded for these two species (mainly for *C. sclopetarius*).

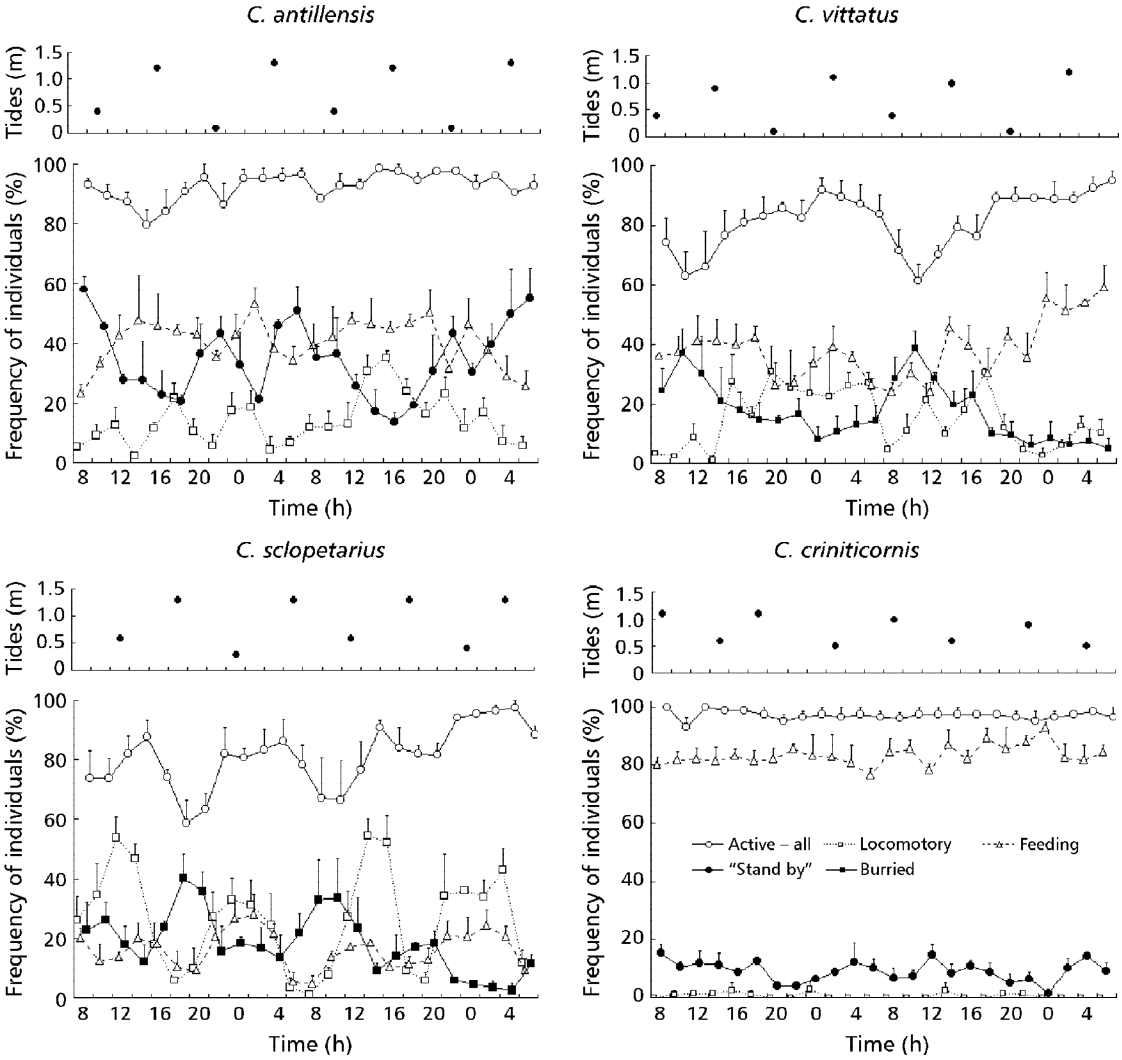

Fig. 1 — Behavioral patterns displayed by the hermit crabs *Clibanarius antillensis*, *C. sclopetarius*, *C. vittatus* and *Pagurus criniticornis* during a 48-hour period. Points are the mean percentage of individuals (+SE) displaying each of the most conspicuous behaviors based on the 3 replicates (pools). Frequency of active individuals are the pooled frequencies of crabs displaying the following behaviors: locomotory, feeding, reproductive, agonistic and 'stand by' – stopped in the sediment surface. The height of high and low tides during the observation period is shown for each species. The periods of the days were characterized as follows: morning – 06:00 to 12:00 h; afternoon – 12:00 to 19:00 h; evening – 19:00 to 20:00 h; night (nocturnal) – 20:00 to 05:00 h; dawn – 05:00 to 06:00 h; available daylight: ±14 h.

Few reproductive and agonistic behaviors were recorded, nor were individuals completely retracted into their shells. The activity pattern of *C. vittatus* could be characterized as evening and nocturnal, with resting peaks during the morning (Fig. 1). Within a 24 h period the activity pattern of *C. sclopetarius* presented two marked inactivity peaks, corresponding to dawn and evening. High activity of this species was recorded in the middle of both the day and the night and was associated with flooding tides. The relationship between activity and tidal cycles was not apparent for *C. vittatus*.

High activity was recorded for *Pagurus criniticornis* during the whole 24h period without evident resting times (Fig. 1). This continuous activity pattern of *P. criniticornis* was associated with high feeding frequency (Fig. 1). This species, differs from the others in that feeding events were interspersed with short-distance displacements. *Pagurus criniticornis* used their ambulatory legs to move over the substrate and their chelipeds to pick up and put particles into their mouths while stopping briefly. The other species clearly stopped in the sediment surface for longer periods while manipulating food than did *P. criniticornis*, thus characterizing a different foraging strategy. The individuals of *P. criniticornis* displaying locomotory behavior, such as that recorded for the other studied species, were limited to those displacing for longer distances without stopping for feeding. This particularity caused a nonsignificant relationship between feeding and locomotory behavior in *P. criniticornis* ($n = 24$; $r = 0.10$; $p = 0.653$). Neither clusters of inactive individuals nor buried crabs were frequently recorded during the experiment. Reproductive displays and agonistic encounters were also rarely observed in this species.

DISCUSSION

The four studied hermit crabs showed consistent patterns of activity in the two days of observation. However, there was an evident activity variation among these species and three distinct patterns could be distinguished. The results indicated that the three species of *Clibanarius* have circadian activity rhythms during a high tide simulated situation while *P. criniticornis* does not. There was no evidence of intrinsic circatidal rhythm for these species, although the bimodal semidiurnal activity pattern of *C. sclopetarius* could support this assumption since the tides are also semidiurnal in the study area. In fact, during the experiment there was a relationship between the high activity periods of *C. sclopetarius* and the flooding tide periods in São Sebastião Channel, as also recorded for *C. digueti* (Snyder-Conn, 1980) and *C. laevimanus* (Gherardi & Vannini, 1993) in nature.

As shown above, activity patterns may vary markedly between and within genera. Such variation was also verified for five genera of Caribbean hermit crabs by Hazlett (1966), who also recorded the activity patterns of *C. antillensis* and *C. cubensis* (synonym of *C. sclopetarius*, see Forest & Saint Laurent, 1967). In this study, Hazlett (1966) demonstrated that *C. antillensis* have high activity at night and an inactivity peak in the middle of the day. These results are very similar to those presented for this species in the present study. However, the activity periods of *C. sclopetarius* described by Hazlett (1966) evidenced an evening feeding peak and a nocturnal aggressive behavior pattern. These results are quite different from the bimodal semidiurnal activity/resting peaks presented by the population studied here and may indicate a geographical variation in the activity pattern of some species. However, the comparisons with the findings of Hazlett (1966) are not conclusive because the activity pattern was not evaluated from 0 to 6 h in his study.

The continuous activity pattern of *P. criniticornis* differed greatly from the highly variable activity patterns recorded for other pagurid species by Hazlett (1966): *P. miamensis* (night peak), *P. pygmaeus* (night peak), *P. bonairensis* (morning peak), and *P. marshi* (morning peak). In addition, *Pagurus samuelis* and *P. granosimanus* showed a marked nocturnal activity pattern when submitted to normal day-night photoperiod without temperature control (Ball, 1968). Since the temperature correlated well with illumination variation, it become difficult to separate temperature effects from those associated with a circadian day-night variation in field and outdoor experiments. However, the shady conditions employed in the present study prevented direct sun-ray access and, as a consequence, maintained the water temperature constant in the experimental pools.

Except for *Pagurus criniticornis*, continuous activity patterns were only recorded for *P. samuelis* and *P. granosimanus* under constant temperature and under both constant illumination or darkness conditions (Ball, 1968), which also indicate the absence of an intrinsic circadian rhythm in these species.

In addition, *Pagurus bernhardus* was more active during the day while the coexisting *P. prideauxi* presented higher activity at night (Mitchell, 1973), with *Paguristes oculatus* showing a diurnal activity pattern (Stachowitsch, 1979).

Each hermit crab species may be characterized by a particular behavioral pattern. In this way, the activity pattern of *C. sclopetarius* and *C. vittatus* may be evidenced not only by the frequency of active individuals but also by that of buried crabs. The burying behavior was characteristic of these two species although some individuals of *C. antillensis* and *P. criniticornis* also buried themselves in the sediment. The low burying frequency in *C. antillensis* may be associated with the fact that this species is typical of consolidated substrates. In contrast, the low burying frequency in *P. criniticornis* does not support field observations during low tides, when almost all individuals of this species are buried in mud (A. Turra, unpublished data). This suggests that burying in this species may be a behavioral response to a tidal cycle and not a resting behavior governed by a daily light/dark variation. Inactive individuals completely retracted into their shells may also characterize the resting time of *C. antillensis*. As this behavior was previously recorded in the field for individuals of this species during low tides (Turra & Leite, 2000; Turra *et al.*, 2000), it seems to follow a circadian rhythm, although a circatidal rhythm may also be involved.

The three species of *Clibanarius* formed clusters, unrecorded for inactive individuals of *Pagurus criniticornis*. These results corroborate field observations on dispersion and clustering patterns of these four hermit crab species in the Araçá region (Turra *et al.*, 2000). Clustering behavior in hermit crabs is well documented in the literature (Snyder-Conn, 1980; Gherardi & Vannini, 1993; Turra & Leite, 2000; Barnes & Arnold, 2001) and is associated with predation and desiccation risks during the periods of high and low tides, respectively. As clustering (or resting) occurred periodically in a constant high tide situation, it is supposed that the occurrence this behavior is independent of tidal cycles. This rationale can be also applied to other behaviors such as burying and retracting into the shells. Since these behaviors are associated with crab inactivity and are influenced by tides (as presented above), the higher frequency of these behaviors during low tides in nature is obvious. Although clustering has been supposed to reduce desiccation risks (Snyder-Conn, 1980; Turra & Leite, 2000) and ultimately may be shown to have other causes (Gherardi & Vannini, 1993), the present data suggest that clustering is not a direct response of hermit crabs to emersion. In addition, in spite of the fact that the occurrence of buried individuals and individuals retracted into their shells was not a direct consequence of tidal cycles, these behaviors may favor survival at low tide as pointed out by Reese (1969) and Taylor (1981).

Despite the experiments having been conducted in the reproductive period of the studied species (Turra & Leite, 2000), reproductive and agonistic behaviors were recorded in low frequencies for all species. This prevented identifying any variation pattern. Hazlett (1966) verified that agonistic/aggressive behavior is positively related to locomotory behavior frequencies for some species. Hazlett (1968) also demonstrated the effect of crowding in the aggressive behavior of *Pagurus bernhardus*, although aggressiveness may be markedly reduced in a few days when crabs are adjusted to the new density levels (Grant & Ulmer, 1974). Thus, the lower density of individuals in the experimental pools and the higher acclimatizing period in the present study in relation to that used by Hazlett (1966) may be responsible for the low aggressive behavior frequencies in the present study. However, the apparent frequency increase in active crabs from the first to the second observation day (see Fig. 1) may suggest that the crabs were still adapting to density even after three days of acclimatizing. This does not invalidate the results since the activity patterns of the studied species were generally consistent during the two subsequent observation days. Finally, as the experimental density of the studied species was higher than what is found in nature (Turra *et al.*, 2000), one would expect a low agonistic encounter level in the field for these species. In the same way, experimental densities may have led to a limited number of encounters and, consequently, to a limited number of mating frequency during the observations.

The activity pattern variation of the studied hermit crabs should be taken into account in the design of further experiments. The duration of experiments with hermit crabs, such as those focussed on shell selection, may vary from 12 h (Grant & Ulmer, 1974) to 24 h or more (Abrams, 1978; Turra & Leite, 2002). Most hermit crab species show activity/inactivity peaks during a 24 h period, i.e., they exhibit circadian rhythms of activity (Hazlett, 1966; present study). Therefore it is recommended that experiments requiring active crabs and especially those in which the data are obtained only at the end of the trials, such as shell selection, should be carried out over at least a 24 h period. Experiments with a minimum duration of 24 h certainly will include active individuals of all the studied species. However, since *P. criniticornis* and *C. antillensis* have a relatively higher activity than the other two species (see Fig. 1), interspecific behavioral comparisons not taking this variation into account may be misleading. Observations during shorter or more restricted periods of time should be made of all species in periods of high activity. In this way, more precise and accurate interspecific behavioral comparisons could be achieved in nocturnal experiments. Species like *P. criniticornis*, which present high activity during a 24 h period, are more suitable for behavioral studies or as educational tools since observations can be made throughout the day.

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