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ACTIVITY PATTERNS OF *Aedes aegypti* AND *Aedes albopictus* (DIPTERA: CULICIDAE) UNDER NATURAL AND ARTIFICIAL CONDITIONS

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ABSTRACT
Different kinds of organisms are exposed to daily natural changes in light/dark and temperature cycles. Such organisms are well adapted to those changes, expressing a specific behavior which is endogenously controlled and also is as a product of the expression of some clock genes. *Aedes aegypti* and *Aedes albopictus* are two important dengue vectors in various countries around the world. The study of the activity rhythm of dengue vectors is crucial to understand better their daily behavior, the dynamics of virus transmission as well as the best application of mechanisms of mosquitoes control. Thus, the objective of this review is to evaluate some studies on the behavior and circadian rhythms of *A. aegypti* and *A. albopictus* under natural and laboratory conditions.
Keywords: *Aedes aegypti*; *Aedes albopictus*; activity; field; laboratory.

RESUMO
PADRÕES DE ATIVIDADE DE *Aedes aegypti* E *A. albopictus* (DIPTERA: CULICIDAE) SOB CONDIÇÕES NATURAIS E DE LABORATÓRIO. Diferentes tipos de organismos estão expostos a alterações diárias nos ciclos ambientais de claro-escuro e de temperatura. Tais organismos são adaptados a essas mudanças, apresentando comportamento específico, que é endogenamente controlado e produto de expressão gênica. *Aedes aegypti* e *Aedes albopictus* são considerados dois importantes vetores da dengue em diversos países do mundo. O estudo do padrão de atividade dos vetores da dengue é crucial para que possamos compreender melhor os seus hábitos comportamentais, a dinâmica de transmissão dos vírus, bem como para a melhor eficiência na aplicação de mecanismos de controle desses vetores. Assim, o objetivo dessa revisão é analisar os estudos já realizados acerca do comportamento e do padrão circadiano de *A. aegypti* e *A. albopictus* em ambientes naturais e de laboratório.
Palavras -chave: *Aedes aegypti*; *Aedes albopictus*; atividade; campo; laboratório.

RESUMEN
PATRONES DE ACTIVIDAD DE *Aedes aegypti* E *A. albopictus* (DIPTERA: CULICIDAE) BAJO CONDICIONES NATURALES Y DE LABORATORIO. Los diferentes tipos de organismos están expuestos a alteraciones diarias en los ciclos ambientales de claro-oscuro y de temperatura. Tales organismos están adaptados a esos cambios, presentando un comportamiento específico, que es controlado endógenamente y es el resultado de la expresión génica. *Aedes aegypti* y *Aedes albopictus* son considerados importantes vectores de dengue en diversos países del mundo. El estudio del patrón de actividad de los vectores de dengue es crucial para que podamos comprender mejor su comportamiento, la dinámica de transmisión de los virus, así como para una mayor eficiencia en la aplicación de mecanismos de control de esos vectores. Es por esto que el objetivo de esta revisión es analizar los estudios ya realizados acerca del comportamiento y el patrón circadiano de *A. aegypti* y *A. albopictus* en ambientes naturales y de laboratorio.
Palabras clave: *Aedes aegypti*; *Aedes albopictus*; actividad; campo; laboratorio.

INTRODUCTION

Since life started on Earth, living organisms of all kinds of organization are essentially exposed daily to changes in light/dark as well as temperature cycles. Many studies have been written describing activity cycles of certain organisms, such as plants, animals and man itself. Such organisms could show some variations in their behavior during the whole day and, for a first moment, those varieties were interpreted as simple answers from the organisms to the environmental cycles that they were exposed to. That is, for the first studies, a plant or a specific animal behavior was explained simply by being exposed to a dark or a light phase or some specific temperature (Moore-Ede *et al.* 1982, Rotenberg *et al.* 1997).

The explanation of biological rhythms as simply a consequence of environmental variation became incontestable for a few decades. Nevertheless, during the XVIII century, a French astronomer called Jean Jacques D´ortous de Mairan made a series of elegant experiments that contested the idea of biological rhythms as simple answers to environmental changes. De Mairan made his studies with the heliotrope *Mimosa pudica*. This heliotrope opens its leaves during the day and closes them during the night. In his study, de Mairan put the heliotrope into a totally closed box, so the plant could not feel the light/dark cycles. Surprisingly, the astronomer verified that the heliotrope continued to open its leaves during the hours that would correspond to the light phase (subjective day) and close them during the hours that would correspond to the dark phase (subjective night). For the first time, the maintenance of a biological rhythm under constant environmental conditions was demonstrated (Moore-Ede *et al*. 1982, Rotenberg *et al*. 1997).

Many other works were done on the persistence of circadian rhythms (rhythms that last about 24 hours) under constant conditions, however, some researchers questioned the role of temperature on circadian rhythms. Thirty years later, in 1759, Duhamel Du Monceau repeated the experiment with the same heliotrope used by Jean de Mairan, but, this time, under highly controlled temperature. The same circadian rhythm was observed demonstrating that the rhythmic leaf movement was independent of temperature (Moore-Ede *et al*. 1982, Rotenberg *et al*. 1997).

In 1832, Augustin de Condolle found that *M. pudica* not only kept opening and closing its leaves on the subjective day and night but it also tended to repeat the cycle a little earlier each day, showing an endogenous period of 22-23 hours. That was the first evidence that an endogenous clock, under constant conditions, free-run and expresses an endogenous period, generally a little earlier or later than 24 hours (Moore-Ede *et al.* 1982, Rotenberg *et al*. 1997).

The new idea of an endogenous clock controlling the circadian rhythms of different organisms raised many questions and, consequently, many experiments trying to prove the opposite, but always just confirming the idea. After so much effort, it is well known nowadays that circadian clocks have three important properties.

The first property of circadian clocks is their timekeeping persistence when isolated from environment cues. Just as the experiment with the heliotrope showed, endogenous clocks still persist without time cues, although not showing a strong 24 hours period anymore. The endogenous period (named tau and represented as *t*) is close, but rarely equal to the environmental periodicity (Marques *et al*. 1997, Clements 1999).

This endogenous period, or free-running period, shows a well-defined homeostasis that keep it unaltered even when exposed to some variation of physical, chemical or biological variables, most notably temperature. This termocompensation is the second property of endogenous clocks (Marques *et al*. 1997, Clements 1999).

The third one is their capacity to synchronize with the environment where they are exposed to. We all are exposed to daily cycles of light/dark that last 24 hours and endogenous clocks are very well adapted to daily function during those 24 hours. Endogenous clocks are well synchronized with time cues, especially the light/dark and temperature cycles, which can be slightly altered during summer or winter days. Light and temperature are the most important time variables that can synchronize the endogenous clock. They can also be called as *zeitgeber*, a German coumpound word which means time giver and refers to environmental signals (Marques *et al.* 1997, Clements 1999).

All organisms show more activity in a specific moment of the day what is really important to make individuals of same species to meet themselves in space and in time. Because of this phase preference of activity, some species can be diurnal, nocturnal or crepuscular. These temporal preferences can be observed among insects, particularly, in mosquitoes.

CIRCADIAN RHYTHMS IN DENGUE VECTORS

Many aspects of mosquitoes´ physiology and behavior, such as daily rhythms of locomotion, flight, feeding and oviposition, are clock controlled. Consequently, those activities are restricted to a particular phase of the day. The study on circadian rhythms of adult mosquitoes has a great importance since many species are implicated as vectors of human diseases, such as *Aedes (Stegomyia) aegypti* (Linnaeus, 1854) and *Aedes (Stegomyia) albopictus* (Skuse 1894).

Aedes aegypti is an African mosquito, first described in Egypt. Rapidly, this species invaded the Americas, probably during the colonial period when slave trades from Africa were highly frequent (Consoli & Lourenço-de-Oliveira 1994). Nowadays, *A. aegypti* has a world wide distribution and also plays an important role in dengue virus transmission in many different countries. In general, *A. aegypti* is considered an urban mosquito, being most frequently found in urban and suburban areas, where the number of houses and human beings are high (Braks *et al.* 2003, Lima-Camara *et al.* 2006). In addition, this mosquito shows an endophilic and anthropophilic behavior, being frequently caught inside houses and feeding on human blood (Scott *et al.* 1993, Thavara *et al.* 2001, Hoeck *et al.* 2003, Lima-Camara *et al.* 2006). The breeding sites of *A. aegypti* larvae and pupae are often artificial containers filled with water, like cisterns, cans, bottles, tires, glass recipients and so on (Consoli & Lourenço-de-Oliveira 1994).

Aedes albopictus is originated from the Asian continent where it plays an important role in dengue virus transmission (Hawley 1988, Gratz 2004, Ponlawat & Harrington 2005). This mosquito was first described in India and invaded the Americas during the 80´s. Nowadays, its distribution ranges from tropical to temperate areas. In general, *A. albopictus* is frequently found in sylvatic areas, where there is high vegetation coverage and low human density (Hawley 1988, Braks *et al.* 2003, Lima-Camara *et al.* 2006). In some countries, like Brazil, *A. albopictus* has never been incriminated as a natural dengue vector although it can successfully be infected and transmit dengue virus under laboratory conditions (Miller & Ballinger 1988, Lourenço-de-Oliveira *et al.* 2003, Castro *et al.* 2004).

A number of studies have been done involving blood-feeding, landing and oviposition behavior of *A. aegypti* and *A. albopictus* females in the field. Such studies provide a great opportunity for evaluating the natural behavior of vector mosquitoes and, consequently, can be potentially used on the development of new solutions for methods of adult control.

CIRCADIAN STUDIES ON Aedes aegypti

In Tanzania, at Dar es Salaan, Trpis *et al.* (1973) observed a diel periodicity in the landing activity of *A. aegypti* on man. A total of 14 captures were done all over the year and human bait was used to attract females. Except for three captures that lasted 24 hours, all remaining captures lasted 15 hours, beginning at 05h a.m. up to 08h p.m.. Interestingly, the authors were able to collect females and males during their study, because males can also be attracted by the presence of blood sources for females. This study showed a bimodal landing activity for males and females, with peaks at sunrise and sunset or occasionally up to 1.5 hours later in the morning or 3 hours earlier in the afternoon. Although further observations are always necessary, the authors considered *A. aegypti* as a diurnal species in the aforementioned locality. Another study in the same area showed that the diel periodicity was the same for nullipars, pars, inseminated or uniseminated females, all predominantly diurnal and bimodal, with sharp peaks at 06-07h a.m. (post-sunrise) and 5-6h p.m. (pre-sunset) (Corbet & Smith 1974).

Mosquito behavior can show slight differences depending on some environmental conditions. For example, in Djakarta, Indonesia, Atmosoedjono *et al.* (1972) studied blood-feeding activity of *A. aegypti* females using human bait. Continuous collections were carried out for about six hours on two consecutive days (0530h a.m. up to 0630h p.m.) and the authors observed a sharp peak of biting behavior in the morning during the dry season. At the end of the rainy season, the morning peak occurred a little later and an increase in biting activity was observed during the afternoon hours. The authors concluded that this apparent shift of biting behavior toward the afternoon hours on wet season could be an important determinant of dengue virus transmission, since in the afternoon hours individuals taking naps would be more exposed to mosquito bites.

Another good example of environmental influence on mosquito behavior is described by Chadee & Martinez (2000). Using human bait, the authors monitored the landing activity of *A. aegypti* indoor and outdoor in both urban and rural sites. Although adults were more frequently collected inside houses in both sites, differences in the pattern of activity between urban and rural sites were detected. The general pattern of landing was trimodal, with peaks at 7h a.m, 11h a.m. and 05h p.m., but a little nocturnal activity was observed in urban sites which was totally absent in rural sites.

The best explanation for this difference is adaptation to light, that is, the effect of an increase in electrical lighting in and around houses which extends the landing periodicity of *A. aegypti* in urban sites. Epidemiologically, this nightfeeding behavior might extend the period that dengue transmission occurs.

Oviposition behavior has great epidemiological importance considering the time that females prefer to lay their eggs. Using ovitraps, Gomes *et al.* (2006) monitored the oviposition behavior of *A. aegypti* females in Minas Gerais, Brazil. The authors found a major egg-laying activity occurring in the end of photophase and in the beginning of scotophase.

It is well known that mosquitoes' circadian rhythms such as flight, locomotion, oviposition and blood-feeding are endogenous controlled and represent the product of expression of some known clock genes. These clock genes expressions have been extensively investigated in the last years and those expressions are frequently compared to what is observed in mosquito's behavior under laboratory conditions, that is, under controlled temperature and photoperiod regimes.

Gomes *et al.* (2006) made a comparative study of the oviposition behavior of *A. aegypti* females in the field and under laboratory conditions and found similar patterns. Whereas in the field more eggs were laid during the end of photophase extending by up to the fourth hour after sunset, in the laboratory, more eggs were dispensed during the end of photophase up to the second hour of scotophase.

Under conditions of almost constant temperature and humidity and fluctuation daylight of approximately 12 hours of light and 12 hours of dark (LD 12:12), Haddow & Gillett (1957) observed that *A. aegypti* showed a regular cycle of oviposition with one major peak of activity in the afternoon. Gillett *et al.* (1959) also verified *A. aegypti* females laying more eggs during the last hours of photophase regardless of being exposed to light/dark cycles of LD 12:12 or LD 16:08 or LD 08:16. This observation indicates that oviposition cycle is well adapted to several changes in light/dark cycles.

Taylor & Jones (1969) made a series of interesting experiments upon inseminated *A. aegypti* females. The authors exposed *A. aegypti* females to different photoperiods, such as LD 12:12, constant dark (DD) and constant light (LL). Under constant conditions, the length of the endogenous period could be calculated and showed about 26 hours in LL and about 22-24 hours in DD. In a LD 12:12 regime, the main peak of flight activity occurred 1-2 hours before lights off and there was an increase of activity in the middle of the photophase. Taylor (1999) verified the flight activity of virgin *A. aegypti* females under LD 12:12, LD 08:16 and LD 16:08. In all tested photoperiods, the pattern of activity was diurnal and bimodal, with a low number of active individuals during the night hours. Peaks occurred in lights on and lights off.

Laboratory experiments with *A. aegypti* were almost always conducted with inseminated females. But, in 1981, Jones verified interesting results by testing the circadian activity of *A. aegypti* females in different mating status. Virgin *A. aegypti* females showed a bimodal pattern of activity, with a small peak following lights on and a main peak occurring in the end of photophase, reaching maximum amplitude in the hour before lights off. Conversely, inseminated *A. aegypti* females expressed much less activity than virgin females. In the first days, inseminated females seemed to show a small peak of activity close to the lights off, however, as the activity level increased on the following days, the pattern became more similar to that observed in virgins. Blood fed virgin *A. aegypti* females showed flight activity little affected, despite of being fully engorged. As for blood fed inseminated

A. aegypti females, they became inactive for the first two days after blood-feeding, but activity was recovered on the subsequent days, during the latter part of photophase. It was noticed that lights on peak was not expressed for blood fed inseminated females.

In general, mosquito females show some significant changes on their pattern of activity when they are inseminated (Klowden 1996). A possible reason is that during copulation, males can transfer to females some proteins and other substances produced by accessory glands that can alter the physiology and behavior of females (Klowden 1999). In fact, such alterations have already been described in other different species of mosquitoes like *Anopheles gambiae* (Jones & Gubbins 1977, 1978) and *A. stephensi* (Rowland 1989). This could explain why just blood fed *A. aegypti* did not show alterations on their level of activity whereas inseminated and blood fed inseminated *A. aegypti* females showed a notable reduction in flight activity.

As mentioned before, *A. aegypti* and *A. albopictus* are two important vectors of dengue and other arbovirus in the world, so that, they have been the subjects of several comparing studies about circadian activities under laboratory conditions. For example, diel sugar-feeding and host-seeking rhythms in *A. aegypti* and *A. albopictus* under LD 16:08 were verified by Yee & Foster (1992). For *A. albopictus*, a diurnal-crepuscular and bimodal pattern of sugar-feeding activity was reported. Same pattern was observed for the host-seeking behavior, but this rhythm had a significantly higher activity throughout the night which accounted for the only difference in the diel distribution of sugar-feeding and host-seeking activities. For *A. aegypti*, sugar-feeding occurred as a bimodal and crepuscular rhythm although this activity persisted throughout day and night. Similar pattern was reported in host-seeking behavior, but with a more gradual increase in evening activity. This difference in sugar feeding and host-seeking distribution during the last third of the day was significant. Comparing both species, the sugar-feeding and host-seeking rhythms were rather similar, except for the notable host-seeking activity throughout the night of *A. albopictus.*

Nevertheless, when exposed to an artificial LD 14:10 photoperiod, both *A. aegypti* and *A. albopictus* females did not show any host-seeking activity during the scotophase, when the lights were totally off (Kawada *et al.* 2005). During photophase, a clear bimodal (for *A. albopictus*) and trimodal (for *A. aegypti*) pattern of activity were reported.

CIRCADIAN STUDIES ON Aedes albopictus

Field studies on diel activity patterns of *A. albopictus* in many countries of Asian continent have reported this species blood-feeding during daylight and rarely during night hours (reviewed by Hawley 1988). In these countries, the pattern was bimodal, with one peak in the sunrise and a major peak occurring in the afternoon (reviewed by Hawley 1988).

In Macao, China, Almeida *et al.* (2005) verified diel activity of *A. albopictus* males and females in the field and also verified a bimodal activity, with one peak in the dawn (0608h a.m.) and one peak in the afternoon (0620h p.m.). Between these two peaks, activity was very low, but never null. Same results were observed on La Reunión island by Delatte *et al*. (2010). These authors reported a bimodal blood-feeding activity for *A. albopictus* females with a morning and a much higher afternoon peaks.

Diel oviposition patterns of *A. albopictus* females were also verified by comparing laboratory and field data (Trexler *et al.* 1996). Under laboratory conditions, the females exhibited a diurnal periodicity in its oviposition behavior. When exposed to an artificial LD 14:10 photoperiod, oviposition activity was initiated in the morning crepuscular phase (7h a.m.) and ceased with the onset of darkness (10h p.m.). A principal broad peak occurred during 12h a.m. and 08h p.m., when 92.2% of eggs were laid. From field experiments, it was determinated that *A. albopictus* oviposits primarily during the day. Nevertheless, under laboratory conditions, no eggs were laid in the total darkness period whereas in the field, *A. albopictus* deposited some eggs when traps were open at night and closed during the day.

Under LD 12:12 in laboratory condition, an unimodal pattern of oviposition activity was observed for *A. albopictus* females (Chadee & Corbet 1999). Oviposition was almost exclusively diurnal, with 97.5% of eggs laid during the full photophase. The oviposition periodicity for *A. albopictus* was well defined with a single late-afternoon peak.

Xue & Barnard (1997) investigated the diel pattern of pupation, emergence and oviposition of *A. albopictus* under LD 14:10 in laboratory. Pupation did not show an apparent daily rhythm, but the emergence was rhythmic showing the highest peak during afternoon, at 04h p.m. They also verified in the first gonotrophic cycle, larger size females laid more eggs during crepuscular hours (08-10h p.m.) and smaller females laid more eggs a little earlier (04-06h p.m.).

Many studies on circadian rhythms of mosquito vectors have lead to extensible amounts of informations about diel activity patterns in different physiological stages of individuals kept under laboratory or field conditions. Even so, it is still an important and interesting subject to be explored. Several clock genes have been discovered and the functions of those already known ones have been investigated. Once understanding the endogenous mechanism of a vector and how it influences the behavior of the insect, we can understand the dynamics of vector-host interaction and explore novel strategies for vector-control. Many more questions still need to be answered and perhaps just as many need to be asked. Effects of temperature cycles, constant environment conditions or different photoperiods on the circadian activity of *A. aegypti* and *A. albopictus* still need to be more investigated and explorated.

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