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Oviposition strategies adopted by gravid *Aedes aegypti* (L.) (Diptera: Culicidae) as detected by ovitraps in Trinidad, West Indies (2002–2006)

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ABSTRACT

Aedes aegypti oviposition strategies were studied weekly over a period of 5 years (2002–2006) in Curepe, Trinidad using modified ovitraps. From a total of 23,293 ovitraps collected, 10,156 were collected in the months of the dry season, with 3041 positive (30%) containing 99,577 *Ae. aegypti* eggs. In contrast, during the wet season from 13,137 ovitraps collected, 10,652 were positive (81.9%), containing 192,209 *Ae. aegypti* eggs. When, the number of eggs collected and the number of positive ovitraps were divided into different egg number categories, <30, 31–60, 61–90 and >91, significantly more eggs (G = 89.6; d.f. = 4; P < 0.001) and more positive ovitraps (P < 0.001) were collected within the <30 eggs range, followed by the egg categories 31–60, 61–90 and >91 eggs. The patterns of oviposition displayed by *Ae. aegypti* during the early, mid and late wet and dry seasons showed a significant (F = 102.8; d.f. = 5; P < 0.002) decline in the number of eggs and oviposition occurrences from the early dry season to the late dry season among egg categories, <30 and 31–60 but no significant (F = 3.98; d.f. = 4; NS) decline in the other egg categories. In contrast, during the early, mid and late wet season, significant (F = 209.8; d.f. = 5; P < 0.02) increases were observed in the number of eggs and positive ovitraps collected among egg categories <30, 31–60, and 61–90 but with similar numbers of eggs and oviposition occurrences recorded within the >91 egg category. These results suggest that the oviposition strategies adopted depend on numerous factors including the physical state of the oviposition site, the presence of eggs from conspecific females, whether the same or different individuals and the number or clutch size already present on the oviposition site. Therefore vector control workers should employ source reduction strategies to remove the small containers which may harbour 1–30 eggs and treat the larger permanent containers like water drums which may contain >60 eggs and may be the sites of superoviposition in nature. These combined strategies can effectively control the vector populations and reduce dengue transmission in *Ae. aegypti* infested countries.

1. Introduction

Gravid *Aedes aegypti* (L.) mosquitoes display numerous oviposition strategies when a suitable site is encountered in the laboratory and in the field including dispersing their eggs from a single batch on successive occasions (Gillett, 1962; Chadee and Corbet, 1990) or in different sites (Fay and Perry, 1965; Chadee and Corbet, 1987), a feature often referred to as "skip oviposition" (Mogi and Morky, 1980). This feature is often exaggerated by a female's tendency to avoid laying on surfaces that already bear her own eggs or those of conspecifics (Chadee et al., 1990).

In addition, Apostal et al. (1994) using randomly amplified polymorphic DNA markers (RAPD-PCR) have shown individual females laid on average of 10.95 eggs per ovitrap in Puerto Rico whereas Colton et al. (2003) using codominant restriction fragment length polymorphism (RFLP) markers found an average of 6.5 families per container, with members of 19 families clustered across multiple containers in Trinidad.

Since *Ae. aegypti* females recognize and avoid substrates already bearing eggs (Chadee et al., 1990; Ganesan et al., 2006), such behaviours reduce the possibility of inter- and intra-specific competition and can lead to the dispersal of females to other containers and to other geographic areas, within its flight range, where oviposition sites may be available. The avoidance behaviour observed among the *Ae. aegypti* mosquitoes has also been demonstrated in the cowpea beetles, *Callopobruclus maculates* (F.) (Ofuya and Agele, 1989), in black-flies *Simulium reptans* L. (Coupland, 1991) and in butterflies (Behan and Schoonhoven, 1978).

Chadee et al. (1990) were the first to report on the act of laying eggs on a substrate which bears eggs laid previously by a conspecific, whether the same or a different individual and coined the term "superoviposition". Work by Apostal et al. (1994) indicated that egg density may also affect the number of eggs deposited by gravid *Ae. aegypti*. Later, Allen and Kline (1998) reported the effects

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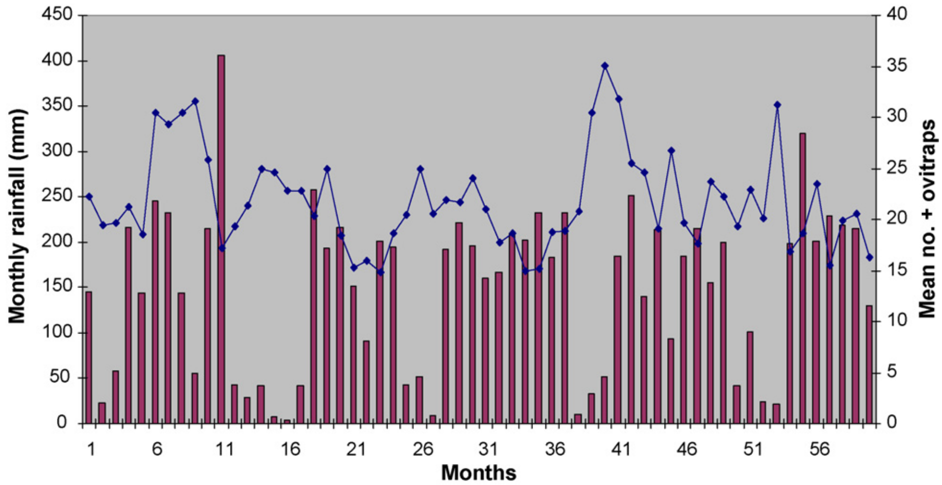

Fig. 1. Seasonal rainfall patterns (bars) and mean number of positive *Ae. aegypti* ovitraps (lines) in Trinidad, West Indies (2002–2006).

of eggs from a prior oviposition on further oviposition in *Ae. aegypti* and *Aedes albopictus* (Skuse). Their results suggested that gravid *Ae. aegypti* mosquitoes preferentially selected substrate where eggs already have been laid.

The selection of suitable oviposition sites by *Ae. aegypti* is a critical factor in their population dynamics and has important implications for vector control measures like source reduction and focal treatment of breeding habitats (Chadee, 1988). Buxton and Hopkins (1927), Chadee et al. (1990) and Apostal et al. (1994) reported that gravid mosquitoes disperse their eggs over several sites with approximately 11–30 eggs per oviposition container. These numbers of eggs have been consistently found in ovitraps (Fay and Eliason, 1966) since their introduction in most countries with *Ae. aegypti* populations (PAHO, 1994). Ovitraps have been used to monitor the population density (Reiter et al., 1991; PAHO, 1994), oviposition periodicity (Chadee and Corbet, 1987), efficacy of insecticide applications (Castle et al., 1999) and the presence or absence of *Ae. aegypti* within the selected areas of countries (PAHO, 1994). However, no studies have been conducted to evaluate routine *Ae. aegypti* ovitrapping data to determine whether egg avoidance, superoviposition or skip oviposition can be gleaned from the proportions of eggs collected on a weekly basis.

This study reviews ovitrap data collected over a 5-year period to determine the extent to which egg avoidance and superoviposition occur in the field. In addition, we examined the results of ovitraps during the wet and dry seasons with a view of identifying key oviposition behaviours, which may assist in surveillance and control or further research on the oviposition behaviour of *Ae. aegypti* mosquitoes.

2. Materials and methods

2.1. Study area

This study was conducted at Curepe (10°42′N; 60°24′W) (a semi-urban area with approximately 3000 houses and 15,000 people) located along the Eastern Main Road to the north and the South Main Road to the west, 16 km east of Port of Spain, the capital of Trinidad. This 5-year study was started in January 2002 and was concluded in December 2006 covering both the wet and dry seasons. The wet season starts in May and ends in November while the dry season starts in December and ends by mid-May. The study area, meteorology, vegetation and population of *Ae. aegypti* have been described by Chadee (2004). Meteorological data were provided by the University of the West Indies Field Station, which is located within 3 km of the Curepe field site.

2.2. Oviposition

The oviposition patterns of *Ae. aegypti* were monitored using modified ovitraps (Fay and Eliason, 1966) as described by Chadee and Corbet (1987). Each ovitrap consisted of a cylindrical, black, glass jar (height 13 cm, diameter 6 cm) containing about 375 ml of tap water and a removable "paddle" – a thin strip of brown hardboard (12.5 cm × 2.5 cm) – on which the mosquitoes laid eggs just above the water level. There was no overflow hole in the side of the jar. Forty-five (45) houses were randomly selected within Curepe and in each house two ovitraps were placed at 1.2 m, one indoors and the other outdoors and serviced weekly as previously described by Chadee (2004).

All 90 ovitraps were exposed for one week for each of 260 weeks from 2nd January 2002 to 31st December 2006. Each week paddles labeled with the site number were removed and replaced by egg-free paddles, the water in each ovitrap discarded, the ovipot scrubbed to remove any eggs laid or attached to the inside surface of the ovitraps (Chadee et al., 1995), and 350 ml of fresh tap water added. The handling of paddles and the identification of eggs after collection were as described by Chadee and Corbet (1987).

The monthly oviposition data and monthly rainfall data were analyzed and compared to determine annual trends. The oviposition patterns were further analyzed separately for the dry season (observations from December to May) and for the wet season (observations from May to November) over the 5-year period. The data from both the wet and dry seasons were further divided into early, mid and late seasons, with December to January being early dry season, February to March being mid dry season and April to May being late dry season. The wet season was similarly divided into early wet season (June to July), mid wet season (August to September) and late wet season (October to November).

During this study, oviposition activity was recorded as the *occurrence of eggs* and the number laid each month. Data were transformed into contingency tables and analyzed using a *G*-test (Sokal and Rohlf, 1981). In addition, the number of eggs laid was transformed ($\sqrt{1+x}$) and an analysis of variance (ANOVA) performed (Sokal and Rohlf, 1981).

3. Results

3.1. Rainfall

Over the 5-year period, a total of 8891.2 mm of rainfall was recorded (see Fig. 1). The heaviest rainfall occurred between the