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Body size-associated survival and dispersal rates of *Aedes aegypti* in Rio de Janeiro

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Abstract. The daily survival rate of *Aedes aegypti* (L) (Diptera: Culicidae) is one of the most important parameters in mathematical models of dengue transmission. In this report, we evaluate the effect of adult body size on the survival and dispersal rates of male and female *Ae. aegypti*, the primary dengue vector in Brazil. Independent of larval diet (i.e. size), the daily survival rate of females recaptured in the field was greater than that of males (smaller: t = 5.617; d.f. = 15; $P < 0.05$; larger: t = 4.241; d.f. = 16; $P < 0.05$). Larger males lived longer than smaller males (t = 2.2893; d.f. = 7; $P < 0.05$), but no size effect was observed for females (t = – 0.086; d.f. = 19; $P = 0.932$). The daily survival rate of smaller females was similar to that of larger females (0.712 and 0.730, respectively, as calculated by an exponential model, and 0.743 and 0.779, respectively, calculated by a non-linear model), and they dispersed further than larger females (mean distances travelled were 78.8 m and 40.9 m, respectively; t = − 10.22; d.f. = 323; $P < 0.05$). Adult body size did not influence male dispersal distances (t = 0.904; d.f. = 206; $P = 0.367$). Given our evidence that smaller females appear to have similar lifespans and evidence from other studies that they bite more frequently during a single gonotrophic cycle than larger females, our results suggest that smaller females have a higher vectorial capacity.

Key words. *Stegomyia*, dengue, diet, size, vectorial capacity, yellow fever, Brazil.

Introduction

Daily survival rate is a key parameter in dengue transmission models (Luz *et al.*, 2003). Vectors must survive for periods longer than the sum of the initial non-feeding period plus the virus's extrinsic incubation period in order to be able to infect another human. For dengue transmission, this usually means ≥ 12 days, given that nulliparous females usually do not blood-feed for ≥ 2 days and the extrinsic incubation period of dengue virus is ≥ 10 days (Kuno, 1995; Salazar *et al.*, 2007).

McDonald (1952) suggested that the daily survival rate of *Aedes aegypti* (L) is constant and independent of age, based on the assumption that mosquitoes die mainly from predation or environmental factors rather than old age. This implies that exponential models should describe time-to-capture data from mark-release experiments, and several studies have since used these models (e.g. Seawright *et al.*, 1977; Reisen *et al.*, 1978, 1980; Costantini *et al.*, 1996). However, one potential bias with the direct application of exponential models to data such as these is that captured individuals are permanently removed from the marked population and this source of population loss is not considered in simple exponential models (Harrington *et al.*, 2001). Noting this, Buonaccorsi *et al.* (2003) proposed a non-linear model that accounts for both sources of loss, but keeps the assumption of age-independent mortality (and age-independent capture rate). Their model showed a better fit to data (from Thailand) than the exponential model.

Besides survival, another important determinant of vectorial potential is dispersal. *Aedes aegypti* is thought to disperse poorly, generally flying 50–300 m from a release point in mark-recapture experiments (Muir & Kay, 1998; Harrington *et al.*, 2001; Tsuda *et al.*, 2001). In some cases, however, longer displacements have been observed (Hausermann *et al.*, 1971; McDonald, 1977; Reiter *et al.*, 1995; Honório *et al.*, 2003). Variation in dispersal distances may be driven by heterogeneity in the availability of oviposition sites and blood-feeding opportunities (Forattini, 1962; Edman *et al.*, 1998; Maciel-de-Freitas *et al.*, 2006a).

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Variation in survival and dispersal (as well as other important components of vectorial capacity, such as fecundity and blood-feeding behaviour) may be partially explained by variation in adult size (Macdonald, 1956; Nasci, 1986a, 1991), which is ultimately a manifestation of larval habitat quality (Nasci & Mitchell, 1994). Inadequate nutrition and/or overcrowding during the larval development of mosquitoes can be associated with reduced adult size, shorter longevity, higher susceptibility to arboviral infections and replication under laboratory conditions (Hawley, 1985; Nasci & Mitchell, 1994; Tun-Lin *et al.*, 2000; Braks *et al.*, 2004; Alto *et al.*, 2005). Smaller females tend to blood-feed more frequently than larger females (Scott *et al.*, 2000), presumably because they emerge with lipid reserves that are often inadequate to develop ovaries to stage II and complete oogenesis from the first bloodmeal (Macdonald, 1956). By contrast, field studies conducted in Louisiana showed that smaller *Ae. aegypti* were not abundant among blood-fed females collected with a battery-powered aspirator, suggesting a higher survival rate for larger individuals (Nasci, 1986a).

Dengue transmission is a serious public health problem in most large cities in Brazil, particularly Rio de Janeiro, a city regarded as lying in the centre of the region where dengue is most endemic and the most significant dissemination point in the country (Lourenço-de-Oliveira *et al.*, 2004). The objective of this study was to test the hypothesis that body size influences survival and dispersal rates of *Ae. aegypti* in a dengue-endemic area of Rio de Janeiro. Two non-overlapping size classes of adults were developed by rearing larvae under poor and rich diet conditions. The survival and dispersal of these individuals were estimated using mark-release-recapture (MRR) methods.

Materials and methods

Study area

The study was conducted in Tubiacanga, a suburban district located at Ilha do Governador, an island in Guanabara Bay in the northeast part of the city of Rio de Janeiro (22°47′08″S, 43°13′36″ W). Tubiacanga is a geographically isolated neighbourhood, limited by Guanabara Bay and runways at the international airport. Because the nearest settlement is 2.1 km away, mosquito emigration is not expected to be important in Tubiacanga, in which approximately 2900 inhabitants live in about 850 houses. In 2005, three cases of dengue were recorded in Tubiacanga; in 2006, up to the 18th ‘entomological week’ (beginning of May), 21 cases of dengue were reported. (For further details on Tubiacanga, see Maciel-de-Freitas *et al.*, 2007a, b).

Wing length of wild mosquitoes

To estimate the distribution of wing length in Tubiacanga’s natural population of *Ae. aegypti*, a sample of 254 females and 311 males was collected with a battery-powered aspirator a few weeks before the experiment began and their wings were measured under a dissecting microscope with an ocular micrometer. Wing length was defined as the distance from the axillary incision to the apical margin excluding the fringe (Harbach & Knight, 1980). Female wing length ranged from 2.25 mm to 3.62 mm (mean ± standard deviation [SD] 2.80 ± 0.29 mm) and followed a normal distribution (Kolmogorov–Smirnov $D = 0.073$; $P < 0.05$). Male wing length ranged from 1.28 mm to 2.75 mm (mean ± SD 1.92 ± 0.31 mm) and featured an approximately normal distribution ($D = 0.048$; $P < 0.05$).

Producing adults in two non-overlapping size classes

The *Ae. aegypti* used in the experiments were derived from a laboratory colony that is routinely renewed with eggs collected in the field in Rio de Janeiro. Larvae for the experiment were reared in laboratory conditions (25 ± 5° C and 60 ± 8% RH) under two distinct diets in order to obtain adults within two non-overlapping wing size intervals.

The poor diet consisted of 1.25 g of fallen avocado leaves, collected from the field, washed, sun-dried for ≥ 2 days, broken into pieces (4-cm^2 maximum), weighed and finally mixed with 1400 mL of unchlorinated water in a plastic basin. This mixture rested for 7 days, and 1.25 g of chitosan, an analogue of insect chitin used to simulate the remains of arthropods, was added to provide a protein component to the larval diet. Groups of 120 *Ae. aegypti* first instar larvae were placed in the plastic basins 7 days after the addition of chitosan. After 12–17 days, the poor diet produced females with a mean ± 2 SD wing length of 2.58 ± 0.22 mm (range 2.36–2.80 mm) and small males with a wing length (mean ± SD) of 1.68 ± 0.16 mm (range 1.52–1.84 mm).

Individuals on the rich diet were raised under the same conditions described above, with a hay infusion substituted for the avocado leaves. To further improve the rich diet, when larvae were 4 days old, an additional 1.25 g of hay infusion was added to the plastic basins. After 10–13 days, the rich diet produced females with a mean ± 2 SD wing length of 2.99 ± 0.14 mm (range 2.85–3.13 mm) and large males with a mean ± SD wing length of 2.02 ± 0.13 mm (range 1.89–2.15 mm). The range of female wing lengths, measured as mean ± 2 SD, did not overlap between diets. However, the range of wing lengths in males showed some overlap, and we opted to use only those with wings in the interval of the mean ± SD. After emergence, adults were provided with a daily 10% sucrose solution until the time of release.

Female wing lengths of laboratory-reared mosquitoes are in accordance with other investigations, which reported small class mean sizes between 2.48 mm and 2.55 mm and amplitude ranging between 2.25 mm and 2.95 mm, and large class mean sizes between 2.96 mm and 3.26 mm, with amplitude ranging between 2.96 mm and 3.40 mm (Nasci & Mitchell, 1994; Naksathit & Scott, 1998).

Mark, release and recapture

Because the day of emergence varied among groups (as a result of the nutritional conditions), mosquitoes were released in batches, as individuals reached 4–5 days old. Marking with fluorescent dust (Day-Glo Color Corp., Cleveland, OH, U.S.A.) was performed < 30 min before release (at 08.00–09.00 hours) in small cylindrical cages, where the fluorescent dust was sprinkled. Fluorescent dust marking is the most commonly used method in MRR experiments and has no effect on mosquito survival or behaviour (Service, 1993; Muir & Kay, 1998; Hagler & Jackson, 2001). Mosquitoes released on different days were marked with different colours of dust.

Recapturing was performed with CDC backpack aspirators and BG-Sentinel (BGS) traps (Clark *et al.*, 1994; Maciel-de-Freitas *et al.*, 2006b). BG-Sentinel traps are baited with a combination of lactic acid, ammonia and caproic acid, substances that are found on human skin. Battery-powered BGS traps generate ascending and descending air flows that attract mosquitoes flying in the vicinity, and have been shown to be an efficient means of capturing host-seeking female *Ae. aegypti* (Maciel-de-Freitas *et al.*, 2007b).

Every day from day 1 after the first release, 15 houses were randomly selected and aspirated for 15–20 min, both indoors and outdoors. Another set of 15 randomly selected houses received one BGS trap each, which was inspected every day. The BGS traps remained installed in the same houses for the entire duration of the study. By chance, aspiration was occasionally carried out in a house where a BGS trap was installed. Daily captures stopped when no dust-marked individuals were collected by any method for 3 consecutive days.

Captured mosquitoes were examined under ultraviolet light to check for the presence of fluorescent dust. Marked mosquitoes were separated by sex, and classified as small or large based on wing length measurements. Four dust-marked captured mosquitoes (three males and one female) had wing lengths that were intermediate between the small and large classes; these were removed from analysis as their size group was unclear.

Survival under laboratory conditions

Thirty recently emerged individuals from each size class and sex were isolated individually in labelled cylindrical plastic vials (6.5 cm height, 2.5 cm diameter) containing moistened cotton overlaid with filter paper on the floor of the vials, as substrate for oviposition. The top was covered with mosquito netting. These adults were kept in the laboratory at $25 \pm 5°$ C and $60 \pm 8\%$ RH (Maciel-de-Freitas *et al.*, 2004) and provided with 10% sucrose solution daily. The RH inside the vials varied from 80% to 85%. Survival rate was measured by counting the number of dead individuals daily. Survival curves of males and females on poor and rich diets were compared by log-rank test (Kleinbaum, 1996). Wing lengths of all dead individuals were measured to check whether they fitted into the appropriate size groups.

Survival in the field

The probability of daily survival (PDS) was estimated by fitting the exponential model (Gillies, 1961) and the removal-corrected model (Buonaccorsi *et al.*, 2003) to capture data for males and females reared on the two diets. The exponential model was fit by least squares, after log-transformation. The non-linear model was fit using non-linear least squares. The slopes of the regression lines of each group (male and female *Ae. aegypti* reared on poor and rich diets) were compared by two-sample *t*-test (Zar, 1999).

The average life expectancy (ALE) was calculated from the lower and upper 95% confidence interval values of PDS evaluated by the non-linear model, as $1/-\log_e \mathrm{PDS}$ and PDS^{10}, respectively (Niebylski & Craig, 1994). Additionally, the proportion of females living for ≥ 10 days, when more than 76% of orally experimentally infected mosquitoes have the virus in the salivary glands (Salazar *et al.*, 2007), was also evaluated. The latter expression provides the estimated proportion of mosquitoes that would survive for long enough to transmit dengue virus. Statistical analyses were performed using the statistical package R 2.3.1 (R Development Core Team, 2006).

Dispersal

Release and recapture data were geo-referenced using a global positioning system (GPS) (Garmin eTrex personal navigator, Garmin International, Inc., Olathe, KS, U.S.A.). All co-ordinates were entered into a geographical information system (GIS), which calculated the distances between release and capture points. Dispersal patterns of *Ae. aegypti* females and males on both diets were summarized by the mean distance travelled (MDT) and the maximum distance travelled (MAX) (Lillie *et al.*, 1981; White & Morris, 1985).

To evaluate the effect of diet and days since release on mosquito dispersal, linear models were fit to male and female data separately, as the behaviour patterns of each sex vary (e.g. males fly to search for females or nectar; females fly to search for oviposition sites, mates, nectar and/or hosts). Goodness-of-fit was evaluated by R^2 values. For all analyses, dispersal distances were log-transformed, as this variable presented non-normal distribution.

Ethical considerations

Mark-release-recapture experimental protocols were submitted to and approved by Fiocruz Ethical Committee (CEP/Fiocruz protocol number 253/04). The potential increase in the risk of disease transmission resulting from the release of female *Ae aegypti* was considered to be negligible, since the numbers to be released were insignificant in relation to the size of the natural population.

Results

Survival under laboratory conditions

Diet did not have an effect on the survival of males (log-rank test: $\chi^2 = 1.7$; d.f. $= 1$; $P = 0.19$) or females ($\chi^2 = 0.5$; d.f. $= 1$; $P = 0.479$) kept in the laboratory (Fig. 1, Table 1). In fact, independently of sex and size, mosquitoes maintained in the laboratory presented high rates of survival (Table 1).

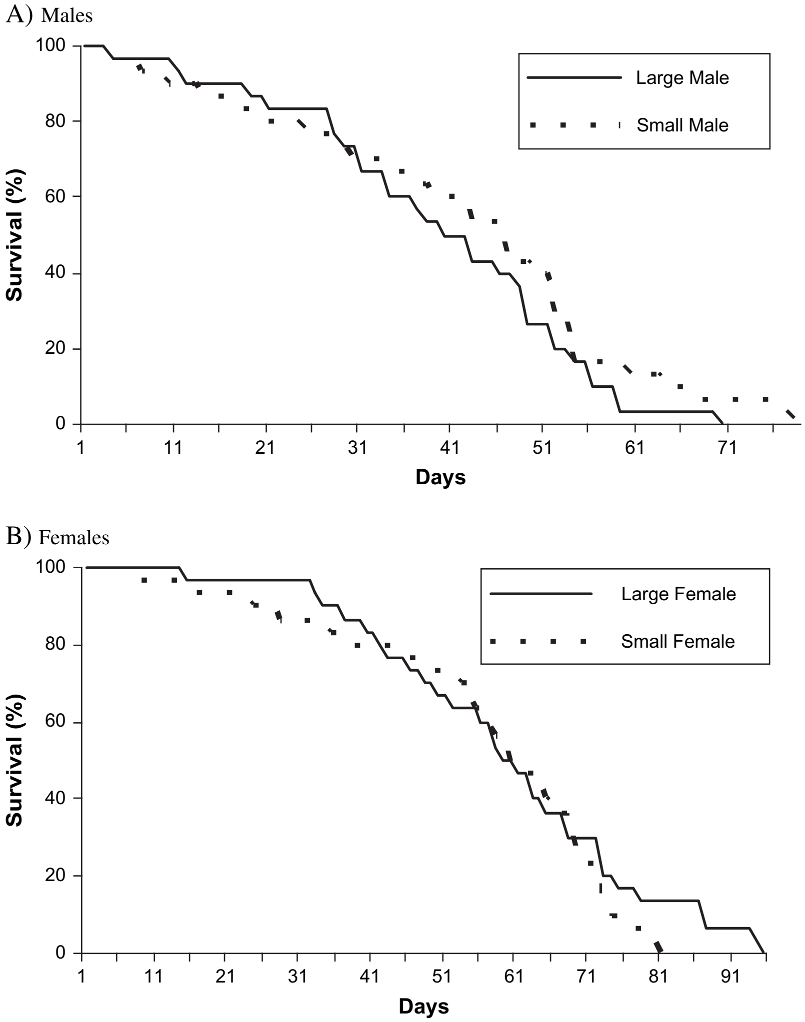

Fig. 1. Survival curves of *Aedes aegypti* males (A) and females (B) fed poor vs. rich diets as larvae to produce small and large adults, respectively, in laboratory conditions. Small male and small female treatments started with 28 and 29 individuals, respectively.

Released and recaptured mosquitoes

Mosquito release and recapture points are shown in Fig. 2. A total of 2818 large adults (51% male) and 2245 small adults (47% male) were released during the study. Recapture rates varied from 7.5% (rich-diet males) to 13.7% (rich-diet females) (Table 1). The recapture effort, measured from the release of the first mosquito group to the last day of collection, lasted 17 days. A higher proportion of the catches in BGS traps, the odour-baited traps, were females, whereas a higher proportion of the CDC backpack aspirator catches were males (Table 2).

Table 1. Summary statistics from the mark-release-capture experiment with male and female *Aedes aegypti* produced from poor vs. rich larval diets.

	Males	Males	Females	Females
	Poor diet	Rich diet	Poor diet	Rich diet
PDS by exponential model under laboratory conditions	0.964	0.956	0.981	0.973
Number of released adults	1059	1427	1186	1391
Recapture rate (%)	12.27	7.35	11.29	13.73
PDS by exponential model for recaptured mosquitoes	0.323	0.525	0.712	0.730
R^2 (exponential model)	0.897	0.955	0.937	0.909
PDS by non-linear model for recaptured mosquitoes	0.411	0.559	0.743	0.779
Interval of survivorship*	0.392–0.431	0.521–0.601	0.716–0.772	0.746–0.817
Daily recapture rate (%)	41.09	6.04	4.21	6.27
Interval of ALE (days)*	1.06–1.18	1.53–1.96	2.99–3.86	3.41–4.94

*Calculated with the 95% confidence interval provided by the Buonaccorsi non-linear method. PDS, probability of daily survival; R^2, coefficient of determination; ALE, average life expectancy.

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Estruturação do mapa: Laboratório de Geoprocessamento/FIOCRUZ

Fig. 2. Points of release and recapture of male and female *Aedes aegypti* with small and large body sizes in Tubiacanga, Rio de Janeiro. Recapture was carried out with CDC backpack aspirators and BG-Sentinel traps in 30 houses per day.

Survival in the field

In field conditions, diet had a significant effect on the survival rates of males, with larger males living longer than smaller males (t = 2.2893; d.f. = 7; $P < 0.05$) (Table 1), but the same was not observed for females (t = – 0.086; d.f. = 19; $P = 0.932$). Overall, the daily survival rate of females was greater than that of males, for both small and large sizes (small: t = 5.617, d.f. = 15, $P < 0.05$; large: t = 4.241, d.f. = 16, $P < 0.05$). The expected daily survival rate of smaller females was estimated to be 0.712 (exponential model) and 0.743 (non-linear model), providing an estimated ALE in the range of 2.99–3.86 days (Table 1). The expected proportion of females living > 10 days therefore is estimated to be in the range of 3.54–7.51%.

Table 2. Number and frequency of recapture of fluorescent dust-marked mosquitoes by BG-Sentinel trap and CDC backpack aspirator in Tubiacanga.

	Males		Males		Females		Females	
	Poor diet		Rich diet		Poor diet		Rich diet	
	n	(%)	*n*	(%)	*n*	(%)	*n*	(%)
BG-Sentinel trap	34	(26.2)	23	(21.9)	93	(69.4)	125	(65.4)
CDC backpack aspirator	96	(73.8)	82	(78.1)	41	(30.6)	66	(34.6)

Mosquitoes had a higher PDS rate under laboratory conditions than in the field (small males: t = 11.31, d.f. = 62, $P < 0.05$; large males: t = 7.042, d.f. = 76, $P < 0.05$; small females: t = 5.627, d.f. = 94, $P < 0.05$; large females: t = 5.545, d.f. = 103, $P < 0.05$) (Table 1, Fig. 3).

Dispersal

The MDT of smaller males (32.02 m) was slightly less than that of larger males (42.16 m), but this difference was not significant (t = 0.904; d.f. = 206; $P = 0.367$) (Table 3, Fig. 4). The MAX of larger males was 131.7 m and that of smaller males was 104.2 m. By contrast, diet had a significant effect on female dispersal. The displacement of smaller females

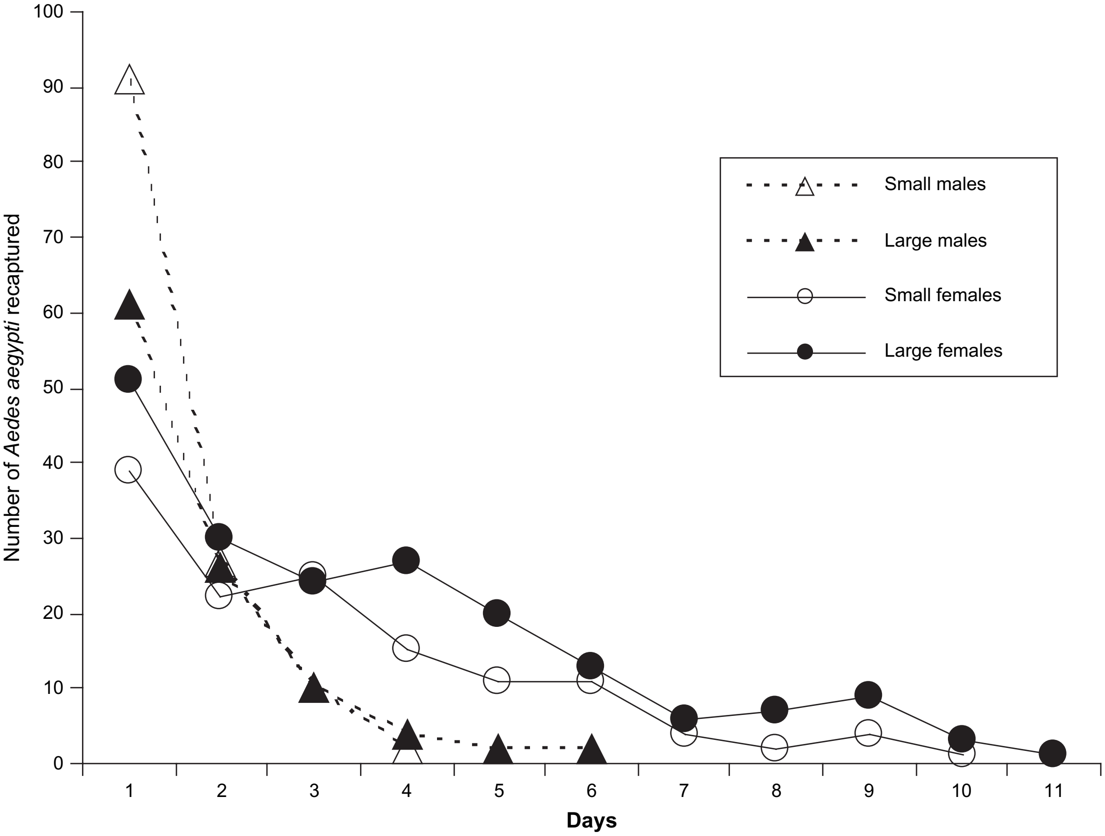

Fig. 3. Number of recaptured *Aedes aegypti* males and females collected per day using backpack aspirators and BG-Sentinel traps as a function of time.

(measured by MDT) was significantly greater than that of larger females (t = –10.22; d.f. = 323; $P < 0.05$; Table 3). In fact, the MDT as a function of time for smaller females was constantly greater than that observed for larger females (Fig. 4). It is interesting to note that for every measure of dispersal distance shown in Table 3, results for males and females reared on rich larval diets were remarkably similar, whereas the values for females reared on poor larval diets were all nearly twice as great.

Table 3. Distances of recapture sites from the release site of dust-marked *Aedes aegypti* caught with backpack aspirators and BG-Sentinel traps in Tubiacanga.

	Males	Males	Females	Females
	Poor diet	Rich diet	Poor diet	Rich diet
MDT (m)	32.02	42.16	78.81	40.94
FR_{50} (m)	18.01	38.95	70.21	36.24
FR_{90} (m)	54.75	81.46	137.32	81.93
MAX (m)	104.2	131.7	203.3	143.2

MDT, mean distance travelled (from release point to site of recapture); FR_{50} and FR_{90}, distance that 50% and 90% of the population dispersed; MAX, maximum distance from release point to site of recapture.

Discussion

This study assessed the effect of body size on the survival and displacement of male and female *Ae. aegypti* in the field, through an MRR experiment. We found that, overall, females tended to live longer than males. Size was a statistically significant determinant of male survival in the field, but apparently not of female survival. Generally, smaller females were caught further away than larger females and larger males, which were caught at remarkably similar distances, whereas smaller males travelled less far than any other group.

Mosquito survival curves in the laboratory were similar to other reports for *Ae. aegypti* maintained in analogous situations (Day *et al.*, 1994; Naksathit & Scott, 1998), but were high compared with those in the field, probably as a result of the climatic stability and reduced force of mortality in the laboratory (no predation, etc.). Variation in wing length at low and high diets was high compared with results from similar studies and may be a consequence of less strict laboratory conditions. It is likely that more rigid control of temperature and RH can produce adults with lower SDs and therefore with lower wing length ranges.

The results of the MRR experiment show that smaller males had a significant higher mortality rate than larger males, probably as a result of the suboptimal diet of the former. Extrapolation

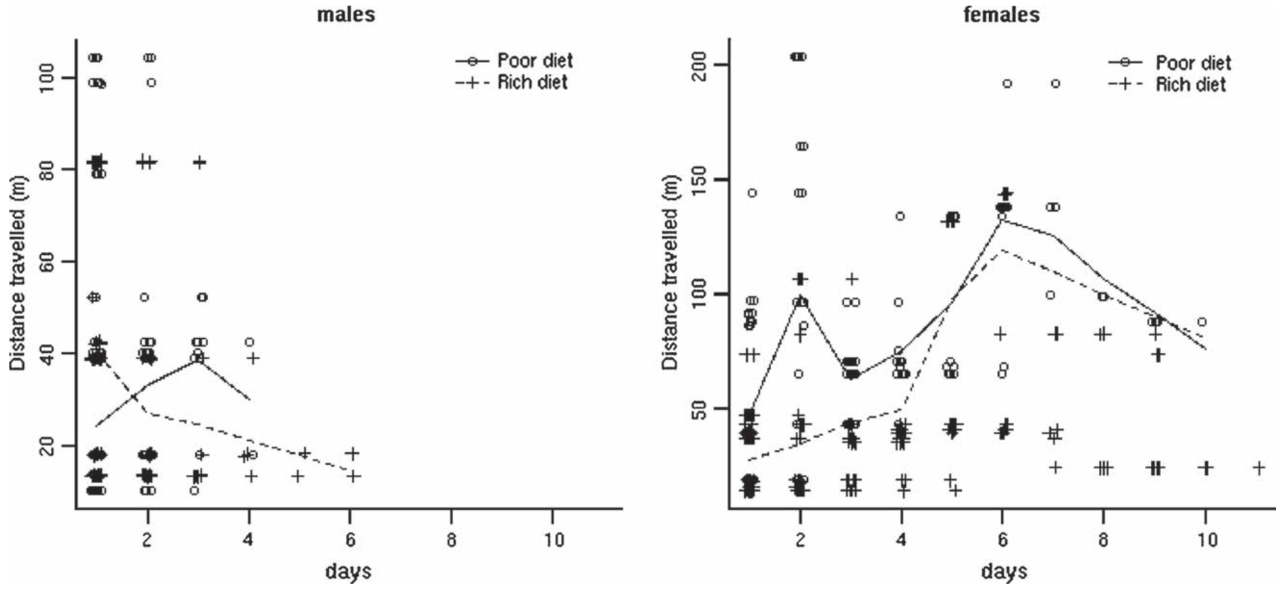

Fig. 4. The effect of diet on the distribution of distance from release site at which *Aedes aegypti* males and females were recaptured as a function of time. The curves indicate 'mean distance travelled' (MDT) for mosquitoes on a poor larval diet (solid lines) and those on a rich larval diet (dashed lines).

of this result to the natural population, noting that small wild males are quite abundant, suggests that development conditions in many containers at Tubiacanga are poor, and that intra- or interspecific competition for resources may be an important force driving *Ae. aegypti* population dynamics in this area (Braks *et al.*, 2004; Honório *et al.*, 2006).

Our results show no difference in survival rates between larger and smaller females, contradicting the general hypothesis that larger females live longer under natural conditions (Nasci, 1986a, b). Discrepancies among experiments can be explained by differences in food sources and other habitat-specific mortality factors. For example, Maciel-de-Freitas *et al.* (2007b) found differences in the survival rates of females in neighbourhoods of Rio de Janeiro with different ambient characteristics, such as availability of human hosts and oviposition sites. Further studies should be undertaken to assess the effect of body size on survival in areas across a range of environmental conditions. Aside from biological factors, the lack of a size effect in females may be attributable to the aggregation of sizes into two classes, and to the experimental design itself (MRR). Further studies should be carried out to validate this finding.

Our observation that survival rates are independent of size for females led us to rethink the role of small females as vectors. It is generally accepted that small females take more bloodmeals per gonotrophic cycle than larger females, thereby increasing the possibility of acquiring and transmitting dengue virus (Scott *et al.*, 2000). Several studies have shown that, in addition to blood-feeding more often, smaller females blood-feed more successfully and are more easily infected than larger females (Day & Edman, 1984; Nasci & Mitchell, 1994; Scott *et al.*, 2000; Alto *et al.*, 2005). If small and large females have the same lifespan, the former may have a greater vectorial capacity.

The ALE values observed for females in Tubiacanga seemed to be lower than the minimum required for virus replication and consequent dengue transmission (Salazar *et al.*, 2007); with our results, only ~ 3–7% of females would have lived long enough to be responsible for virus transmission (Maciel-de-Freitas *et al.*, 2007b; Salazar *et al.*, 2007).

Recently, it was proposed that *Ae. aegypti* has a limited dispersal ability in Rio de Janeiro (Costa-Ribeiro *et al.*, 2006a, b; Maciel-de-Freitas *et al.*, 2007b), and that both males and females disperse only short distances from a release point (Harrington *et al.*, 2005). Our results agree with these findings, and suggest that smaller females disperse further than males. In addition, male and female dispersal rates were differently affected by diet. Although smaller individuals must have less energy reserves than larger mosquitoes, and therefore a more limited dispersal capacity (Briegel *et al.*, 2001; Briegel, 2003), we found that smaller females dispersed over greater distances, presumably as a result of their more frequent host-seeking activity.

Mark-release-recapture experiments are valuable tools for probing the life history of insects in the wild. Unfortunately, biases may arise from this type of experiment, especially when working with animals the size of mosquitoes. Recapture rates for mosquitoes tend to be lower than those for larger animals and possibly decrease with time, as mosquitoes disperse to larger areas. The sampling design we used in this study (random choice of recapture sites) allowed the comparison of diet groups, but we stress that a better understanding and estimation of insect movement overall will require new technologies, such as the development of microchips and long-distance monitoring tools for small animals.

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References

Alto, B.W., Lounibos, L.P., Higgs, S. & Juliano, S.A. (2005) Larval competition differentially affects arbovirus infection in *Aedes* mosquitoes. *Ecology*, **86**, 3279–3288.

Braks, M.A.H., Honório, N.A., Lounibos, L.P., Lourenço-de-Oliveira, R. & Juliano, S.A. (2004) Interspecific competition between two invasive species of container mosquitoes, *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae), in Brazil. *Annals of the Entomological Society of America*, **97**, 130–139.

Briegel, H. (2003) Physiological bases of mosquito ecology. *Journal of Vector Ecology*, **28**, 1–11.

Briegel, H., Knüsel, I. & Timmermann, S.E. (2001) *Aedes aegypti*: size, reserves, survival, and flight potential. *Journal of Vector Ecology*, **26**, 21–31.

Buonaccorsi, J.P., Harrington, L.C. & Edman, J.D. (2003) Estimation and comparison of mosquito survival rates with release-recapture-removal data. *Journal of Medical Entomology*, **40**, 6–17.

Clark, G.G., Seda, H. & Gubler, D.J. (1994) Use of the 'CDC backpack aspirator' for surveillance of *Aedes aegypti* in San Juan, Puerto Rico. *Journal of the American Mosquito Control Association*, **10**, 119–124.

Costantini, C., Li, S., Torre, A.D., Sagnon, N., Coluzzi, M. & Taylor, C.E. (1996) Density, survival and dispersal of *Anopheles gambiae* complex mosquitoes in a West African Sudan savanna village. *Medical and Veterinary Entomology*, **10**, 203–219.

Costa-Ribeiro, M.C.V., Lourenço-de-Oliveira, R. & Failloux, A.B. (2006a) Geographic and temporal genetic patterns of *Aedes aegypti* populations in Rio de Janeiro, Brazil. *Tropical Medicine and International Health*, **11**, 1276–1285.

Costa-Ribeiro, M.C.V., Lourenço-de-Oliveira, R. & Failloux, A.B. (2006b) Higher genetic variation estimated by microsatellites compared to isoenzyme markers in *Aedes aegypti* from Rio de Janeiro. *Memórias do Instituto Oswaldo Cruz*, **101**, 917–921.

Day, J.F. & Edman, J.D. (1984) Mosquito engorgement on normally defensive hosts depends on host activity patterns. *Journal of Medical Entomology*, **21**, 732–740.

Day, J.F., Edman, J.D. & Scott, T.W. (1994) Reproductive fitness and survivorship of *Aedes aegypti* (Diptera: Culicidae) maintained on blood, with field observations from Thailand. *Journal of Medical Entomology*, **31**, 611–617.

Edman, J.D., Scott, T.W., Costero, A., Morrison, A.C., Harrington, L.C. & Clark, G.G. (1998) *Aedes aegypti* (Diptera: Culicidae) movement influenced by availability of oviposition sites. *Journal of Medical Entomology*, **35**, 578–583.

Forattini, O.P. (1962) *Entomologia Médica*, Vol. 1, pp. 185–302. Universidade de São Paulo, São Paulo.

Gillies, M.T. (1961) Studies on the dispersion and survival of *Anopheles gambiae* Giles in East Africa, by means of marking and releasing experiments. *Bulletin of Entomological Research*, **52**, 99–127.

Hagler, J.R. & Jackson, C.G. (2001) Methods for marking insects: current techniques and future prospects. *Annual Review of Entomology*, **46**, 511–543.

Harbach, R.E. & Knight, K.L. (1980) *Taxonomist's Glossary of Mosquito Anatomy*, pp. 1–54. Plexus Publications Co., Marlton, NJ.

Harrington, L.C., Buonaccorsi, J.P., Edman, J.D., Costero, A., Kittayapong, P., Clark, G.G. & Scott, T.W. (2001) Analysis of survival of young and old *Aedes aegypti* (Diptera: Culicidae) from Puerto Rico and Thailand. *Journal of Medical Entomology*, **38**, 537–547.

Harrington, L.C., Scott, T.W., Lerdthusnee, K. *et a*l. (2005) Dispersal of the dengue vector *Aedes aegypti* within and between rural communities. *American Journal of Tropical Medicine and Hygiene*, **72**, 209–220.

Hausermann, W., Fay, R.W. & Hacker, C.S. (1971) Dispersal of genetically marked female *Aedes aegypti* in Mississippi. *Mosquito News*, **31**, 37–51.

Hawley, W.A. (1985) The effect of larval density on adult longevity of a mosquito, *Aedes sierrensis*: epidemiological consequences. *Journal of Animal Ecology*, **54**, 955–964.

Honório, N.A., Cabello, P.H., Codeço, C.T. & Lourenço-de-Oliveira, R. (2006) Preliminary data on the performance of *Aedes aegypti* and *Aedes albopictus* immatures developing in water-filled tyres in Rio de Janeiro. *Memórias do Instituto Oswaldo Cruz*, **101**, 225–228.

Honório, N.A., Silva, W.C., Leite, P.J., Gonçalves, J.M., Lounibos, L.P. & Lourenço-de-Oliveira, R. (2003) Dispersal of *Aedes aegypti* and *Aedes albopictus* (Diptera: Culicidae) in an urban endemic dengue area in the State of Rio de Janeiro, Brazil. *Memórias do Instituto Oswaldo Cruz*, **98**, 191–198.

Kleinbaum, D.G. (1996) *Survival Analysis: a Self-Learning Text*, pp. 45–82. Springer Verlag, New York, NY.

Kuno, G. (1995) Review of the factors modulating dengue transmission. *Epidemiological Review*, **17**, 321–335.

Lillie, T.H., Marquardt, W.C. & Jones, R.H. (1981) The flight range of *Culicoides mississippiensis* (Diptera: Ceratopogonidae). *Canadian Entomologist*, **113**, 419–426.

Lourenço-de-Oliveira, R., Vazeille, M., Filippis, A.M.B. & Failloux, A.B. (2004) *Aedes aegypti* in Brazil: genetically differentiated populations with high susceptibility to dengue and yellow fever viruses. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **98**, 43–54.

Luz, P.M., Codeço, C.T., Massad, E. & Struchiner, C.J. (2003) Uncertainties regarding dengue modelling in Rio de Janeiro, Brazil. *Memórias do Instituto Oswaldo Cruz*, **97**, 871–878.

Macdonald, W.W. (1956) *Aedes aegypti* in Malaya. II. Larval and adult biology. *Annals of Tropical Medicine and Parasitology*, **50**, 399–414.

Maciel-de-Freitas, R., Brocki-Neto, R.W., Gonçalves, J.M., Codeço, C.T. & Lourenço-de-Oliveira, R. (2006a) Movement of dengue vectors between human-modified environment and an urban forest in Rio de Janeiro. *Journal of Medical Entomology*, **43**, 1112–1120.

Maciel-de-Freitas, R., Codeço, C.T. & Lourenço-de-Oliveira, R. (2007b) Daily survival rates and dispersal of *Aedes aegypti* females in Rio de Janeiro, Brazil. *American Journal of Tropical Medicine and Hygiene*, **76**, 659–665.

Maciel-de-Freitas, R., Eiras, A.E. & Lourenço-de-Oliveira, R. (2006b) Field evaluation of effectiveness of the BG-Sentinel, a new trap for capturing adult *Aedes aegypti* (Diptera: Culicidae). *Memorias do Instituto Oswaldo Cruz*, **101**, 321–325.

Maciel-de-Freitas, R., Gonçalves, J.M. & Lourenço-de-Oliveira, R. (2004) Efficiency of rubidium marking in *Aedes albopictus* (Diptera: Culicidae): preliminary evaluation on persistence of egg labelling, survival, and fecundity of marked females. *Memórias do Instituto Oswaldo Cruz*, **99**, 823–827.

Maciel-de-Freitas, R., Marques, W.A., Peres, R.C., Cunha, S.P. & Lourenço-de-Oliveira, R. (2007a) Variation in *Aedes aegypti* (Diptera: Culicidae) container productivity in a slum and a suburban district of Rio de Janeiro during dry and wet seasons. *Memórias do Instituto Oswaldo Cruz*, **102**, 489–496.

McDonald, G. (1952) The analysis of sporozoite rate. *Tropical Disease Bulletin*, **49**, 569–585.

McDonald, P.T. (1977) Population characteristics of domestic *Aedes aegypti* (Diptera: Culicidae) in villages on the Kenya coast. II. Dispersal within and between villages. *Journal of Medical Entomology*, **14**, 49–53.

Muir, L.E. & Kay, B.H. (1998) *Aedes aegypti* survival and dispersal estimated by mark-release-recapture in northern Australia. *American Journal of Tropical Medicine and Hygiene*, **58**, 277–282.

Naksathit, A.T. & Scott, T.W. (1998) Effect of female size on fecundity and survivorship of *Aedes aegypti* fed only human blood versus human blood plus sugar. *Journal of the American Mosquito Control Association*, **14**, 148–152.

Nasci, R.S. (1986a) The size of emerging and host-seeking *Aedes aegypti* and the relation of size to blood-feeding success in the field. *Journal of the American Mosquito Control Association*, **2**, 61–62.

Nasci, R.S. (1986b) Relationship between adult mosquito (Diptera: Culicidae) body size and parity in field populations. *Environmental Entomology*, **15**, 874–876.

Nasci, R.S. (1991) Influence of larval and adult nutrition on biting persistence in *Aedes aegypti* (Diptera: Culicidae). *Journal of Medical Entomology*, **28**, 522–526.

Nasci, R.S. & Mitchell, C.J. (1994) Larval diet, adult size, and susceptibility of *Aedes aegypti* (Diptera: Culicidae) to infection with Ross River virus. *Journal of Medical Entomology*, **31**, 123–126.

Niebylski, M.L. & Craig, G.B. (1994) Dispersal and survival of *Aedes albopictus* at a scrap tire yard in Missouri. *Journal of the American Mosquito Control Association*, **10**, 339–343.

R Development Core Team (2006) *R: A Language and Environment for Statistical Computing,* R Foundation for Statistical Computing, Vienna.

Reisen, W.K., Aslam, Y., Siddiqui, T.F. & Khan, A.Q. (1978) A mark-release-recapture experiment with *Culex tritaeniorhincus* Giles. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **72**, 167–177.

Reisen, W.K., Mahmood, F. & Parveen, T. (1980) *Anopheles culicifacies* Giles: a release recapture experiment with cohorts of known age with implications for malaria epidemiology and genetical control in Pakistan. *Transactions of the Royal Society of Tropical Medicine and Hygiene*, **74**, 307–317.

Reiter, P., Amador, M.A., Anderson, R.A. & Clark, G.G. (1995) Short report: Dispersal of *Aedes aegypti* in an urban area after blood-feeding as demonstrated by rubidium-marked eggs. *American Journal of Tropical Medicine and Hygiene*, **52**, 177–179.

Salazar, M.I., Richardson, J.H., Sánchez-Vargas, I., Olson, K.E. & Beaty, B.J. (2007) Dengue virus type 2: replication and tropisms in orally infected *Aedes aegypti* mosquitoes. *BMC Microbiology*, **7**, 9.

Scott, T.W., Amerasinghe, P.H., Morrison, A.C., Lorenz, L.H., Clark, G.G., Strickman, D., Kittayapong, P. & Edman, J.D. (2000) Longitudinal studies of *Aedes aegypti* in Thailand and Puerto Rico: blood-feeding frequency. *Journal of Medical Entomology*, **37**, 89–101.

Seawright, J.A., Dame, D.A. & Weidhaas, D.E. (1977) Field survival and ovipositional characteristics of *Aedes aegypti and* their relation to population dynamics and control. *Mosquito News*, **37**, 62–70.

Service, M.W. (1993) *Mosquito Ecology – Field Sampling Methods*, pp. 652–751. Chapman & Hall, London.

Tsuda, Y., Takagi, M., Wang, S., Wang, Z. & Tang, L. (2001) Movement of *Aedes aegypti* (Diptera: Culicidae) released in a small isolated village on Hainan Island, China. *Journal of Medical Entomology*, **38**, 93–98.

Tun-Lin, W., Burkot, T.R. & Kay, B.H. (2000) Effects of temperature and larval diet on development rates and survival of the dengue vector *Aedes aegypti* in north Queensland, Australia. *Medical and Veterinary Entomology*, **14**, 31–37.

White, D.J. & Morris, C.D. (1985) Bionomics of anthropophilic Simuliidae (Diptera) from the Adirondack Mountains of New York State, USA. *Journal of Medical Entomology*, **22**, 190–199.

Zar, J.H. (1999) *Biostatistical Analysis*, 4th edn, pp. 360–375. Prentice Hall, London.

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