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Ecological interactions in *Aedes* species on Reunion Island

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Abstract. Two invasive, container-breeding mosquito species, *Aedes aegypti* (*Stegomyia aegypti*) and *Aedes albopictus* (*Stegomyia albopicta*) (Diptera: Culicidae), have different distribution patterns on Reunion Island. *Aedes albopictus* occurs in all areas and *Ae. aegypti* colonizes only some restricted areas already occupied by *Ae. albopictus*. This study investigates the abiotic and biotic ecological mechanisms that determine the distribution of *Aedes* species on Reunion Island. Life history traits (duration of immature stages, survivorship, fecundity, estimated finite rate of increase) in *Ae. aegypti* and *Ae. albopictus* were compared at different temperatures. These fitness measures were characterized in both species in response to competitive interactions among larvae. *Aedes aegypti* was drastically affected by temperature, performing well only at around 25 °C, at which it achieved its highest survivorship and greatest estimated rate of increase. The narrow distribution of this species in the field on Reunion Island may thus relate to its poor ability to cope with unfavourable temperatures. *Aedes aegypti* was also more negatively affected by high population densities and to some extent by interactions with *Ae. albopictus*, particularly in the context of limited food supplies. *Aedes albopictus* exhibited better population performance across a range of environmental conditions. Its ecological plasticity and its superior competitive ability relative to its congener may further enhance its invasion success on Reunion Island.

Key words. Invasion success, larval competition, life history traits.

Introduction

During biological invasions, the establishment phase depends on the invader's interactions with the abiotic and biotic environments (Shea & Chesson, 2002; Lockwood *et al.*, 2008). Characteristics of both the invading species and the environment invaded can affect the success of the invasion

(Lockwood *et al.*, 2008). Invasive species are more likely to establish in environments that are similar to their native environments, but invaders may also evolve to become better adapted to the invaded environment (Lockwood *et al.*, 2008). Species exhibiting high phenotypic plasticity or ecological flexibility are more likely to become established (Nylin, 1998; Facon *et al.*, 2004). In areas in which the invader's niche

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is already occupied, the most competitive species should be at an advantage compared with less competitive species. Competitive interactions commonly determine distribution, population dynamics and community structure in insects (Denno *et al.*, 1995; Reitz & Trumble, 2002). Effects of competition can include reductions in fecundity, growth and survivorship (Begon *et al.*, 2006). Interspecific competition can lead to competitive displacement of a local population (Reitz & Trumble, 2002) when competing species are too similar in their niche requirements. Container-dwelling mosquitoes that share resources in the larval stages represent a good model for investigating the roles of competitive interactions, particularly in invasive species.

Aedes aegypti (L.) (*Stegomyia aegypti*) and *Aedes albopictus* (Skuse) (*Stegomyia albopicta*) are invasive species in many regions of the globe (Lounibos, 2002). Both species are vectors of arboviruses, including dengue and Chikungunya virus (Gratz, 2004). In the past 40 years, *Ae. albopictus* has invaded all continents except Antarctica and is present today in at least 30 countries (Benedict *et al.*, 2007). The introduction and spread of this mosquito has resulted from the intercontinental shipment of tyres containing eggs, which can survive for long periods because they are relatively highly resistant to desiccation (Hawley, 1988). Understanding the invasive ability of *Ae. albopictus* requires understanding of how its ecological plasticity facilitates its colonization of multiple habitats and of how its physiological plasticity facilitates its establishment in tropical and temperate areas (Hawley, 1988; Paupy *et al.*, 2009). Laboratory and field experiments have demonstrated that *Ae. albopictus* is superior in competition to many resident species (reviewed by Lounibos, 2002; Juliano, 2009). *Aedes aegypti*, which is native to Africa, is widespread in tropical and subtropical areas between the latitudes of 45 ° N and 35 ° S (Christophers, 1960). *Aedes aegypti* spread to the Americas centuries ago via the slave trade (Tabachnik & Powell, 1979) and to Asia more recently via international trade. The widely distributed species *Ae. aegypti* is closely associated with human population and is primarily anthropophilic (Tabachnik & Powell, 1979). *Aedes aegypti* is invasive in many parts of the world, and exhibits high fecundity and an intrinsic rate of increase, and thus good colonization ability (Christophers, 1960).

Successful invasions by *Ae. albopictus* and *Ae. aegypti* have resulted in distributions that overlap. These mosquitoes have similar larval ecological niches and often share the same larval habitats. In the U.S.A., declines in the distribution and abundance of *Ae. aegypti* have followed invasions by *Ae. albopictus*, leading to the hypothesis of competitive displacement between these species (Hobbs *et al.*, 1991; O'Meara *et al.*, 1995). Interspecific competition between these species in North America (Juliano, 1998; Juliano *et al.*, 2004) and South America (Braks *et al.*, 2004) is strong in the field, and is consistent with the hypothesis that interspecific competition has caused the decline of some local populations of *Ae. aegypti*. The issue of how *Ae. aegypti* persists in some areas after invasion remains to be resolved (Juliano, 2009). In Asia, competition following *Ae. aegypti* invasion has suggested an advantage for *Ae. aegypti* over *Ae. albopictus*, at least in some areas (Chan, 1971). The role of competition

between *Ae. aegypti* and *Ae. albopictus* in population replacement thus appears to vary across the globe, suggesting a degree of context-dependent advantage, and therefore must be investigated in particular ecological contexts in order to generate understanding of the distributions of these vectors (Juliano, 2009).

On Reunion Island, both invasive species were described for the first time at the beginning of the 20th century; *Ae. aegypti* is considered to have been the species introduced first (Bagny *et al.*, 2009). Their combined presence is of ecological interest as the island provides a novel ecological context for their interaction. On Reunion Island, the distributions of these species differ greatly. *Aedes albopictus* is present everywhere. The successful invasion by *Ae. albopictus* of Reunion Island suggests that this species is well adapted to the local environment. It has high fecundity over a wide range of temperatures, colonizes urban and rural environments, uses artificial and natural water-holding containers (Delatte *et al.*, 2008, 2009), and feeds on chickens, goats and humans (Delatte *et al.*, 2010). By contrast, the distribution of *Ae. aegypti* on the island has declined dramatically with the expansion of *Ae. albopictus* (Bagny *et al.*, 2009). A population of *Ae. aegypti* persists, but is restricted to rock pools on the drier western coast of the island. There are no data on the mechanisms implicated in the decline of *Ae. aegypti* populations.

We tested three non-mutually exclusive main hypotheses that may explain the differential distributions of these species on Reunion Island: (a) local populations of *Ae. aegypti* are more poorly adapted to the abiotic environment (temperature and humidity) than is *Ae. albopictus*, leading to their occurrence in some isolated, more suitable environments; (b) density dependence is more pronounced in *Ae. aegypti* than in *Ae. albopictus* (we will focus particularly on density-dependent larval mortality (Legros *et al.*, 2009), and (c) biotic interactions, particularly interspecific competition, have more drastic effects on *Ae. aegypti*, contributing to its decline.

The present study aims to contribute to better understanding of the mechanisms that may have led to the distributions observed on Reunion Island, focusing on the responses of the species to abiotic conditions (specifically, temperature) and to biotic impacts (specifically, food deprivation, and intra- and interspecific interactions). First, we test for effects of temperatures on life history traits in *Ae. aegypti* as no data exist on this subject, and compare those effects with those observed in local populations of *Ae. albopictus* as described by Delatte *et al.* (2009). We then characterize fitness measures for several populations of *Ae. aegypti* and *Ae. albopictus* in response to competition among larvae, and test whether the dynamics of these populations exhibit density dependence, and whether interspecific competition is asymmetric, with a strong advantage for *Ae. albopictus*. Investigating these biotic interactions is also of public health importance (Lambrechts *et al.*, 2010) as larval interspecific competition may affect the resulting longevity and fecundity of adults (Reiskind & Lounibos, 2009), as well as vector–pathogen interactions in adult mosquitoes (Alto *et al.*, 2005).

Materials and methods

Study area and collection sites

Reunion Island (21 °06' S, 55 °36' E) is a French island (2500 km²) in the Indian Ocean, situated 1000 km east of Madagascar and 300 km west of Mauritius. Its climate is subtropical and has two distinct seasons, including a cool, dry winter from May to October, and a warmer, rainy summer from November to April. Its topographic features include mountains in the centre that rise to a maximum height of 3000 m a.s.l., generating microclimates that vary from rainy on the east coast to drier on the west coast.

Biological material and rearing conditions

Mosquitoes (*Ae. aegypti* and *Ae. albopictus*) used for the different experiments came from a laboratory colony maintained for three generations and derived from individuals collected in the larval stages in a large number of rock holes in gullies in the western part of Reunion Island. Adults were fed twice per week for 1 h on anaesthetized mice in accordance with the U.S. National Institutes of Health Guide for the Care and Use of Laboratory Animals, under a protocol approved by the Direction des Services Vétérinaires of Reunion Island.

Aedes aegypti life history traits at five different temperatures

Experiments in life history traits in *Ae. aegypti* were conducted as described by Delatte *et al.* (2009) for *Ae. albopictus* on Reunion Island in order to facilitate comparisons between findings in the two species. Constant experimental temperatures (15 ± 1 °C, 20 ± 1 °C, 25 ± 1 °C, 30 ± 1 °C and 35 ± 1 °C) were maintained in environmental chambers (Sanyo MLR-350; Sanyo Electric Co. Ltd, Osaka, Japan) under a photoperiod of LD 12 : 12 h and relative humidity (RH) of 75 ± 10%.

Egg hatchability and incubation period. Five-day-old eggs deposited on wet paper and incubated at 20 °C and 75% RH prior to the experiment were used. At each temperature, 10 papers each with 10 eggs were put into a plastic container filled with 100 mL dechlorinated water supplemented with 1 mg of brewer's yeast (Acros Organic™, Geel, Belgium). Eggs were left in water for 5 days and numbers of hatching larvae were recorded daily. After 5 days, eggs were removed from the water and dried for 2 days. This procedure was repeated three times [to cause hydric stress (Hawley, 1988)]; at the end of the experimental period, unhatched eggs were considered not viable.

Larval stage survivorship and developmental time. For each temperature tested, larval development was studied in 10 replicates of 10 larvae each. Larvae aged <2 h were isolated

in groups of 10 in containers filled with 100 mL dechlorinated water supplemented with 2.5 mg of brewer's yeast (Acros Organic™). Larvae were fed daily with an increasing amount of brewer's yeast depending on instar stage (0.25 mg per L1, 0.50 mg per L2, 0.75 mg per L3 and 1.00 mg per L4). Survivorship rates and developmental times from L1 to adult were evaluated at each temperature. The proportions of females emerging were also determined.

Adult demographic parameters. After emergence from larvae reared at 25 °C, females and males of the same age (<6 h) were placed in pairs within small cages (15 × 7 × 5 cm) maintained at the different temperatures under study. Thirty pairs were individually followed at each temperature. In each cage, a piece of cotton soaked in 10% sugar solution and a cylindrical egg-laying device (4.5 × 1.5 cm) were provided. Every day, a bloodmeal was offered to females from an anaesthetized mouse placed in the cage for 1 h; the number of females that fed was recorded. The number of eggs laid was counted daily and the egg-laying paper was replaced. This treatment lasted until the death of the female, when one wing was removed and measured to test for a relationship between wing length and fecundity. Adult life history components were computed using standard methods (Ebert, 1999) and included life expectancy at birth (i.e. longevity), gross reproductive rates (i.e., fecundity), and the estimated finite rate of increase (λ) [see Eqn. (1)]. Confidence intervals for demographic parameters were estimated as the 2.5 and 97.5 percentiles of a bootstrap distribution resampled 1000 times (Efron & Tibshirani, 1993). For the demographic parameters, the assumption of a 1 : 1 sex ratio was used. The pre-bloodmeal period was considered as the period from adult emergence until the first bloodmeal. The frequency of bloodmeals is an epidemiological parameter used to approximate biting rates of mosquitoes. It was calculated as the average number of bloodmeals taken during the entire lives of females even if no oviposition occurred.

Statistical analyses. For *Ae. aegypti*, differences in egg hatching rates at different temperatures, survival rates from L1 to adult, and proportions of fed females were tested using a pairwise proportion test corrected for multiple tests (Benjamini & Hochberg, 1995; BH correction). Median development times from egg to L1 and from L1 to adult, respectively, were compared among temperatures using a pairwise Wilcoxon test with BH correction. Differences in numbers of bloodmeals were investigated using a pairwise Wilcoxon test.

Experiments on competitive interactions

Experimental cages. The experiments were conducted in mosquito breeders (Bioquip Products, Inc., Rancho Dominguez, CA, U.S.A.) filled with 200 mL of a mixture of water and bamboo infusion. The bamboo infusion was obtained from 3 g of dried cut bamboo leaves (3 × 3 cm) infused in 1 L of water for 15 days at 25 °C. In these experiments, we followed the

Table 1. Experimental conditions used to investigate effects of different densities, diets, treatments and species presence on larval development and adult traits in *Aedes aegypti* and *Aedes albopictus*.

Diet: 1 mg/larvae	Optimal: every 2 days beginning on day 1 Limited: every 7 days beginning on day 15
Total density (both species)	20 40 60
Treatment, % of individuals, single species	100% <i>Ae. albopictus</i> 100% <i>Ae. aegypti</i>
mixed species	50% <i>Ae. albopictus</i> + 50% <i>Ae. aegypti</i>

Each combination of density, diet and treatment was replicated four times.

development of larvae (initially aged ≤ 2 h) under different treatments at 25 °C (Table 1). Optimal and limited diet regimes differed in the frequency at which food was added to the larval habitats. Under the optimal diet regime, food (Tetramin® fish food) was provided on the first day of the experiment and then every 2 days, which should be sufficient for all individuals (L. B. Beilhe, personal observation, 2008), whereas under the limited diet regime the same food was provided 15 days after the beginning of the experiment and every 7 days thereafter. The addition of animal protein into larval habitats that are primarily based on leaf detritus can eliminate interspecific competition and modify the intensity of the interaction (Daugherty *et al.*, 2000). Each day the number of pupae was counted to evaluate the median time to pupation (P50). Emerged adults were sexed and identified. Survivorship of immature stages was calculated for each container and species by dividing the total number of adults of each species by the initial number of larvae of each species.

A composite index of population performance was calculated to estimate the per capita rate of increase (r) of the population (Livdahl & Sugihara, 1984). The modified index $\lambda = \exp(r)$ (Juliano, 1998), which estimates finite rate of increase, was used here to produce estimates for analysis when there was no emergence of females. Cohort growth is indicated when λ is > 1 , whereas a λ of < 1 indicates cohort decline (Juliano, 1998). We calculated λ for each species within each replicate as:

$$\lambda' = \exp \left[\frac{\ln \left[\left(\frac{1}{N_0} \right) \sum_x A_x f(W_x) \right]}{D + \left[\sum_x x A_x f(W_x) / \sum_x A_x f(w_x) \right]} \right] \quad (1)$$

where r (Livdahl & Sugihara, 1984) is in brackets, N_0 is the initial number of females in the cohort (assumed to be 50% of the initial number of larvae), A_x is the number of females emerging on day x , w_x is the measure of mean wing length (in mm) in females emerging on day x , $f(w_x)$ is a function relating daily wing length and production of eggs, and D is the time between adult emergence and reproduction (assumed to be 10 days in both species). The relationship between fecundity and wing

length was investigated in the Reunion Island populations and identified as $f(w_x) = 127.63 w_x - 249.21$ ($R^2 = 0.46$, $n = 12$, $P = 0.016$) for *Ae. albopictus* and as $f(w_x) = 248.53 w_x - 584.22$ ($R^2 = 0.81$, $n = 17$, $P < 0.0001$) for *Ae. aegypti*.

Statistical analyses. Data for pupation time (P50), estimated finite rate of increase, survivorship and female wing length did not meet the assumption of normality, and transformations did not eliminate this problem. For each species, we used generalized linear models with binomial error for survivorship, and Poisson error for all other dependent variables, with the factors of diet (optimal diet, limited diet), treatment (single species, mixed species), covariate density (20, 40 and 60) and all interactions as independent variables. Quasi family was used to counterbalance overdispersion in the model (McCullagh & Nelder, 1989). For each species, we tested separately the effects of significant factors and covariates on the parameters of pupation time (P50), estimated finite rate of increase, survivorship and female wing length using an analysis of covariance (ANCOVA). Following the ANCOVA, Wilcoxon tests were performed to compare the adjusted means between levels of significant factors. The sex ratios for both species in all treatment combinations were compared with the expected value of 50% by proportion test. All statistical analyses were performed using R Version 2.9.0© 2009 (R Foundation for Statistical Computing, Vienna, Austria).

Results

Effects of temperature variation on Ae. aegypti life traits

Life table, survivorship, development time of pre-imaginal stages. *Aedes aegypti* exhibited a constant egg hatching rate of $\sim 70\%$ in temperatures between 15 °C and 30 °C (pairwise proportion test, $P > 0.05$), dropping below 60% only at 35 °C. The average time to egg hatching (4.5 days) did not differ significantly among temperatures (pairwise Wilcoxon test, $P > 0.05$) (Table 2). Survivorship from L1 to adulthood was drastically affected by temperature (Table 2). The best survivorship (61%) was observed at 25 °C, but was greatly lowered ($\sim 33\%$) by an increase or decrease of 5 °C around this optimum. At extreme temperatures (15 °C and 35 °C) *Ae. aegypti* largely failed to reach adulthood (Table 2). The duration of development from L1 to adulthood significantly increased as temperatures decreased (pairwise Wilcoxon test, $P < 0.05$) ranging from 5 days at 35 °C to 29 days at 15 °C (Table 2). Only one adult emerged at 35 °C. The shortest development time determined for multiple adults was 8.2 days at 30 °C (Table 2). Sex ratios ranged from 38% to 50% and thus did not significantly differ from 50% (binomial test, $P > 0.05$) (Table 2).

Demographic parameters. Demographic parameters were not calculated at 15 °C as no oviposition occurred at this

Table 2. Development time and survival rate of immature stages of *Aedes aegypti* and *Aedes albopictus* (including egg stages).

Temperature, °C	Species	Egg–L1		L1–adult		
		Incubation period, days	Hatching rate, %	Development time, days	Survival rate, %	Sex ratio, %
15	<i>Ae. aegypti</i>	5.3 ± 0.4 ^a	77.0 ^a	29.0 ± 2.0*	2.0 ^a	50.0
	<i>Ae. albopictus</i>	7.4 ± 1.8	8.0	35.0 ± 0.9	50.0	47.5
20	<i>Ae. aegypti</i>	4.0 ± 0.3 ^a	74.0 ^a	12.7 ± 0.3 ^a	32.0 ^b	40.0
	<i>Ae. albopictus</i>	2.9 ± 0.4	67.0	14.4 ± 0.4	77.5	43.5
25	<i>Ae. aegypti</i>	3.9 ± 0.3 ^a	72.0 ^a	9.3 ± 0.3 ^b	61.0 ^c	38.0
	<i>Ae. albopictus</i>	4.5 ± 0.7	49.0	10.4 ± 0.7	76.0	41.0
30	<i>Ae. aegypti</i>	4.7 ± 0.1 ^a	69.0 ^a	8.2 ± 0.4 ^b	33.0 ^b	42.0
	<i>Ae. albopictus</i>	6.7 ± 0.7	49.0	8.8 ± 0.6	67.5	46.3
35	<i>Ae. aegypti</i>	4.7 ± 0.4 ^a	45.0 ^b	5.0 ± NA*	1.0 ^a	100*
	<i>Ae. albopictus</i>	7.1 ± 0.8	51.0	12.3 ± 0.7	2.5	66.6

*Statistical differences could not be investigated because the sample size was too small. Different letters (in a column) refer to significant differences in development time and survival rate between temperatures for *Ae. aegypti* (Wilcoxon test). [Data for *Ae. albopictus* were obtained from Delatte *et al.* (2009).] For sex ratio, the absence of a letter means that values did not differ significantly from 50% (proportion test). NA, not available.

Table 3. Demographic parameters in *Aedes aegypti* and *Aedes albopictus* at four constant temperatures.

Parameter	Units	Species	20 °C	25 °C	30 °C	35 °C
Expectation of life at age 0 (e_0)	Days	<i>Ae. aegypti</i>	13.27 (9.57–17.28)	19.52 (15.71–23.68)	11.02 (7.67–14.81)	3.42 (0.53–6.71)
		<i>Ae. albopictus</i>	25.8 (22.8–29.3)	17.9 (16.1–19.8)	19.5 (17.1–22.1)	5.03 (5.02–5.04)
Gross reproductive rate	Eggs/♀	<i>Ae. aegypti</i>	9.62 (3.53–17.29)	69.53 (21.43–151.51)	15.06 (7.81–23.88)	2.44 (0.00–5.74)
		<i>Ae. albopictus</i>	60.39 (12.93–116.62)	150.80 (109.64–191.88)	195.03 (154.66–224.01)	20.19 (11.03–30.16)
Finite rate of increase (λ)		<i>Ae. aegypti</i>	0.99 (0.96–1.02)	1.11 (1.06–1.15)	1.06 (1.01–1.09)	0.63 (0.61–0.65)
		<i>Ae. albopictus</i>	1.07 (1.04–1.09)	1.15 (1.13–1.16)	1.168 (1.152–1.181)	0.90 (0.88–0.91)

Confidence intervals were estimated as the 2.5 and 97.5 percentiles of a bootstrap distribution resample 1000 times. [Data for *Ae. albopictus* were obtained from Delatte *et al.* (2009).]

temperature. Most demographic parameters reached their maximum at 25 °C (Table 3). The population estimated finite rate of increase was also greatest at 25 °C (Table 3). Confidence intervals for gross reproductive rate (GRR) and λ at 25 °C were similar to those at 30 °C (Table 3). The biggest difference occurred between 25 °C and 20 °C and was attributable to fecundity that was seven times lower at 20 °C (Table 3). At 20 °C, the *Ae. aegypti* population was not projected to increase or decline because the estimated finite rate of increase was very close to 1.0 (Table 3). As the overlap in confidence intervals indicates, there were no significant differences between demographic parameters at 20 °C and 30 °C (Table 3). At 35 °C, the population was projected to decrease based on the estimated finite rate of increase.

Pre-bloodmeal period and numbers of bloodmeals. Blood-feeding in *Ae. aegypti* took place only between 20 °C and 35 °C (Table 4); the pre-bloodmeal periods at 20 °C and 30 °C were similar, at around 5 days (Wilcoxon test, $P > 0.05$). The minimum time required for egg laying was 1 day at 35 °C. The number of bloodmeals taken did not differ among temperatures between 20 °C and 35 °C (Wilcoxon test, $P > 0.05$) (Table 4), but small proportions of engorged females laid eggs.

Effects of competitive interactions on Ae. aegypti and Ae. albopictus life traits

Effect of competition on mean pupation time. Mean pupation time in both species was influenced by the factor diet only ($F_{1,43} = 203.04$, $P < 0.0001$ and $F_{1,40} = 138.90$, $P < 0.0001$ for *Ae. albopictus* and *Ae. aegypti*, respectively). In the optimal diet condition, both species developed at least four times faster than in the limited diet condition (Wilcoxon test, $P < 0.0001$ for both species). *Aedes aegypti* ($P50 = 17.3$ days and $P50 = 5.3$ days under the limited and optimal diets, respectively) also developed significantly (Wilcoxon test, $P = 0.043$) faster than *Ae. albopictus* ($P50 = 20.6$ days and $P50 = 5.6$ days under the limited and optimal diets, respectively).

Effects of competition on estimated finite rate of increase. For *Ae. albopictus*, only diet significantly affected the estimated finite rate of increase (Table 5). Population growth was significantly lower in the limited diet condition for *Ae. albopictus* (Wilcoxon test, $P < 0.0001$) (Fig. 1). For *Ae. aegypti*, this growth parameter was affected by the interaction between diet and treatment, and by diet (Table 5). In the single-species treatment, there was a significant difference in

Table 4. Average time (in days) for pre-bloodmeal period (PBM) for *Aedes aegypti* females and mean number of bloodmeals (BM) per females at four temperatures.

Temperature, °C	Species	<i>n</i>	PBM, days, mean ± SD	Min	BM, <i>n</i> , mean ± SD
15	<i>Ae. aegypti</i>	0	0	–	0
	<i>Ae. albopictus</i>	15	15	–	1.3 ± 0.1
20	<i>Ae. aegypti</i>	19	6.4 ± 2.8 ^a	3	1.8 ± 0.3 ^a
	<i>Ae. albopictus</i>	23	5.3 ± 1.3	3	1.6 ± 0.2
25	<i>Ae. aegypti</i>	23	5.1 ± 1.2 ^{ab}	3	2.0 ± 0.3 ^a
	<i>Ae. albopictus</i>	27	5.5 ± 1.2	3	3.3 ± 0.4
30	<i>Ae. aegypti</i>	20	5.1 ± 1.2 ^{ab}	2	2.1 ± 0.3 ^a
	<i>Ae. albopictus</i>	23	4.1 ± 1.18	2	4.3 ± 0.5
35	<i>Ae. aegypti</i>	13	3 ± 0.8 ^b	1	1.4 ± 0.2 ^a
	<i>Ae. albopictus</i>	18	10.8 ± 0.8	1	1.5 ± 0.2

Different letters (in a column) refer to significant differences between temperature conditions (Wilcoxon test).

n, number of blood-feeding females; min, minimal period of time recorded for the PBM. [Data for *Ae. albopictus* were obtained from Delatte *et al.* (2009).]

SD, standard deviation.

Table 5. Results of analysis of covariance (ANCOVA) for λ under competition conditions in *Aedes albopictus* and *Aedes aegypti*.

	<i>Ae. albopictus</i>			<i>Ae. aegypti</i>		
	d.f.	<i>F</i> -value	<i>P</i> -value	d.f.	<i>F</i> -value	<i>P</i> -value
Diet	1	386.30	<0.0001	1	42.49	<0.0001
Treatment	1	0.81	0.3728	1	2.32	0.1364
Density	1	0.17	0.6791	1	2.98	0.0926
Diet : treatment	1	1.06	0.3096	1	36.56	<0.0001
Diet : density	1	0.01	0.8997	1	0.83	0.3675
Treatment : density	1	3.13	0.0855	1	2.64	0.1127
Diet : treatment : density	1	0.33	0.5669	1	0.00	1.0000
Error	42	–	–	43	–	–

Effects significant at $\alpha = 0.05$ are indicated in bold type.

estimated finite rates of increase between the two diet conditions (Wilcoxon test, $P = 0.002$), with the lowest value occurring under the limited diet. Under the optimal diet regime in the single-species treatments, the estimated finite rate of increase was typically just below 1.0 (averaging 0.90 ± 0.12) as a result of the huge decline observed at the density of 60 individuals (Fig. 1). Under the limited diet regime, this parameter averaged 0.54 ± 0.15 (Fig. 1). In the mixed-species treatment, the estimated finite rate of increase differed significantly between the two diet conditions (Wilcoxon test, $P < 0.0001$), and was similar in the optimal diet condition to that in *Ae. albopictus* in the limited diet condition (Fig. 1). Estimated finite rates of increase for *Ae. aegypti* were >1 (1.05 ± 0.16) in the optimal diet condition, leading to an expectation of population growth, whereas these values were uniformly equal to zero in the limited diet condition whatever the density considered (Fig. 1).

Effects of competition on survivorship. For both species, survivorship was significantly affected by diet ($F_{1,43} = 84.81$, $P < 0.0001$ and $F_{1,44} = 59.85$, $P < 0.0001$ for *Ae. albopictus* and *Ae. aegypti*, respectively). There were no effects of the interaction, density or treatment. For both *Aedes* species, survivorship was significantly lower (Wilcoxon test, $P < 0.0001$)

under restricted food conditions (0.17 ± 0.05 and 0.45 ± 0.05 for *Ae. aegypti* and *Ae. albopictus*, respectively) than in the optimal food condition (0.68 ± 0.03 and 0.91 ± 0.02 for *Ae. aegypti* and *Ae. albopictus*, respectively). Survivorship in *Ae. albopictus* was always greater than that in *Ae. aegypti* (Wilcoxon test, $P < 0.0005$). Heterogeneity in survivorship increased in the limited diet condition.

Effects of competition on female wing length. Female wing length in *Ae. albopictus* was affected by diet only ($F_{1,11} = 278.11$, $P < 0.0001$). Mean female wing length was significantly greater under the optimal than the limited diet regime (Wilcoxon test, $P = 0.002$) (Fig. 2A). Female wing length in *Ae. aegypti* was significantly affected by diet ($F_{1,11} = 157.79$, $P = 0.0002$), density ($F_{1,11} = 28.36$, $P = 0.006$), treatment ($F_{1,11} = 11.97$, $P = 0.026$), and the interaction between diet and treatment ($F_{1,11} = 9.95$, $P = 0.034$) (Fig. 2B, C). Mean female wing length was significantly greater in the optimal than in the limited diet condition (Wilcoxon test, $P = 0.002$) (Fig. 2B). No egg laying occurred in the limited diet condition as the minimum female wing length required for egg laying (2.26 mm, calculated from the relationship established in the laboratory) was not achieved in this condition. In the limited diet condition, mean wing length was significantly lower in the

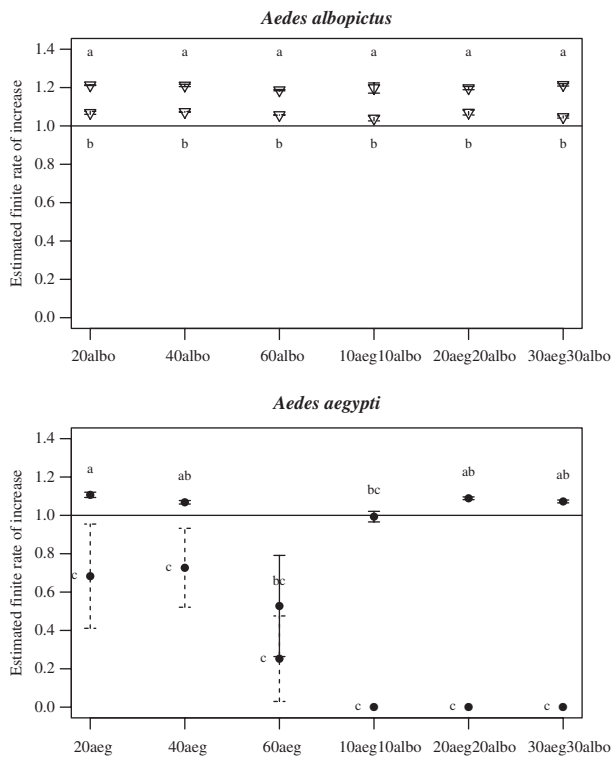


Fig. 1. Mean \pm standard error estimated finite rate of increase (λ) in *Aedes albopictus* and *Aedes aegypti* at 25 °C in each diet condition (optimal diet in solid lines, limited diet in dashed lines), treatment and density combination. Means sharing the same letter do not differ significantly (Wilcoxon test, $P > 0.05$).

mixed-species treatment than in the single-species treatment (Wilcoxon test, $P = 0.038$). When larval density increased, female wing length tended to decrease (Fig. 2C).

Effects of interactions on sex ratio. No effects on sex ratio were seen for *Ae. aegypti* (proportion test, $P > 0.05$) (Table 6). In *Ae. albopictus*, under the optimal diet condition, the sex ratio was close to 50% except at the highest density in the single-species treatment, in which a significantly greater proportion of males emerged (proportion test, $P = 0.007$). In the limited diet condition, the sex ratio was around 50% in the mixed-species treatment, but was female-biased under all densities in single-species treatments (proportion test, $P < 0.05$) (Table 6).

Discussion

The results of the present investigations into life history traits in *Ae. aegypti* at different temperatures and life history traits in both species under competitive interactions contribute to our understanding of differences between these species in their patterns of distribution on Reunion Island. *Aedes aegypti* exhibited traits that differ from those commonly expected for this species throughout the tropics and subtropics. *Aedes*

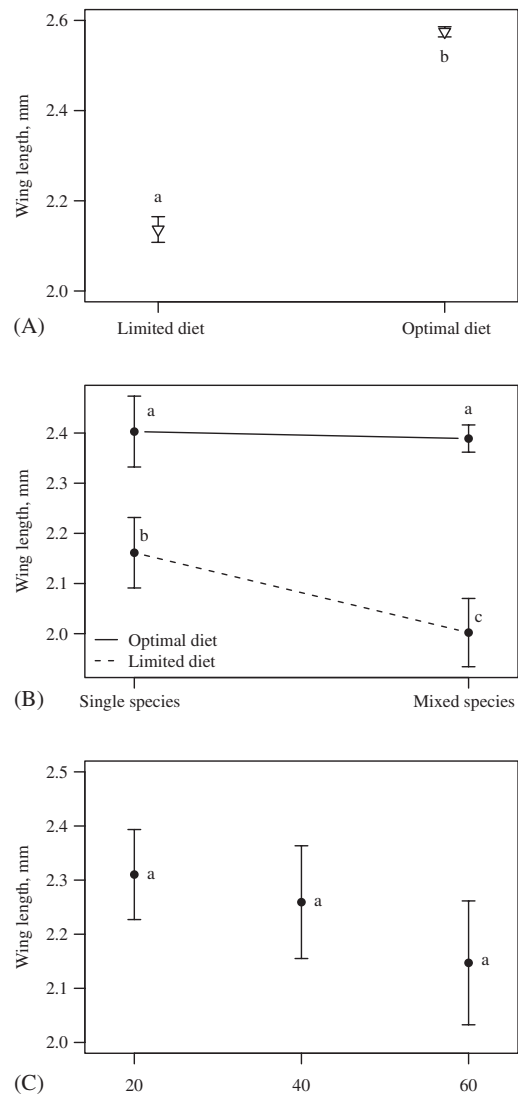


Fig. 2. Effects of significant factors on mean \pm standard error wing length at 25 °C. (A) Effect of diet (limited, optimal) on *Aedes albopictus*. (B) Interaction of treatment (single species, mixed species) and diet (limited, optimal) on *Aedes aegypti*. (C) Effect of density (20, 40, 60) on *Ae. aegypti*. Means within a panel sharing the same letters do not differ significantly (Wilcoxon test, $P > 0.05$).

aegypti was very sensitive to temperature and demonstrated that 25 °C represented the only favourable temperature for larval stages (60% survival rate from L1 to adulthood) and for adult longevity (around 19.5 days). Worldwide populations of *Ae. aegypti* (in the U.S.A., Thailand, Australia and Argentina) generally exhibit higher survival rates from L1 to adulthood (Rueda *et al.*, 1990; Tun-Lin *et al.*, 2000; Tejerina *et al.*, 2009). Populations from Reunion Island were found to be sensitive to low temperatures, as are most other populations (Christophers, 1960; Clements, 2000; Chang *et al.*, 2007), but were surprisingly intolerant of high temperatures. The total fecundity (GRR) and intrinsic rate of increase of the Reunion Island population were always lower than those presented

Table 6. Sex ratios in *Aedes albopictus* and *Aedes aegypti* under different treatments.

	Density	Optimal diet		Limited diet	
		<i>Ae. albopictus</i>	<i>Ae. aegypti</i>	<i>Ae. albopictus</i>	<i>Ae. aegypti</i>
With conspecifics	20	50.0% (74)	48.5% (66)	68.9% (45)*	75.0% (20)
	40	54.4% (147)	58.3% (96)	90.5% (42)‡	54.3% (35)
	60	40.6% (219)†	50.0% (136)	71.2% (52)†	55.1% (49)
With heterospecifics	20	57.1% (35)	61.5% (26)	40% (15)	40.0% (10)
	40	46.3% (67)	53.3% (60)	51.3% (39)	52.9% (17)
	60	58.6% (111)	55.6% (90)	61.4% (44)	50.0% (12)

Sex ratios that differ significantly from 0.5: * $P < 0.05$; † $P < 0.01$, and ‡ $P < 0.001$ (test of equal proportion).

Sex ratios were calculated from the number of individuals that emerged (indicated in brackets).

in data reported in the literature whatever the temperature (Scott *et al.*, 2000; Strickman, 2006; Grech *et al.*, 2010). Development time from L1 to adulthood (9.3 days at 25 °C) was the only life history trait for which findings in our population did not differ greatly from those described in other reports (Tun-Lin *et al.*, 2000; Grech *et al.*, 2010). The current limited distribution and low abundance of *Ae. aegypti* on Reunion Island seem to reflect intrinsically poor adaptation to the abiotic environment, particularly to temperature. Indeed, all demographic parameters (larval and adult) in *Ae. aegypti* were poorer than those in *Ae. albopictus* except for developmental time (shorter in *Ae. aegypti*) and egg survivorship (better in *Ae. aegypti*). Adult demographic parameters in these species were similar only at 25 °C, whereas at 20 °C and 30 °C *Ae. albopictus* demonstrated better population performance in terms of longevity, fecundity and population rate of increase. The major differences between these species in demographic parameters and temperature tolerance may account in part for their differential distribution on an island characterized by the presence of many microclimates.

From an epidemiological point of view, these species also present important differences that may contribute to their roles in the transmission of disease. Whatever the temperature, there were always more females of *Ae. albopictus* that fed and laid eggs. Females of this species fed 1.5 times and twice as often as *Ae. aegypti* females at 25 °C and 30 °C, respectively. This phenomenon has also been observed in Indonesia, although only under low temperatures (Soekiman *et al.*, 1984). Given that once the virus has disseminated from the midgut to the salivary glands of the mosquito, the infected mosquito is capable of transmitting the virus (Vazeille *et al.*, 2003), it is likely that the greater biting rate of *Ae. albopictus* renders it better able to transmit arboviruses on Reunion Island. Indeed, on this island, *Ae. albopictus* lives in more anthropogenic areas than *Ae. aegypti* (Delatte *et al.*, 2008; Bagny *et al.*, 2009), which further suggests that this species is the more likely to trigger human epidemics of arboviruses on the island.

In investigations into competition, *Ae. albopictus* seemed to be less affected by inter- and intraspecific competitive interactions; this species' survivorship, fecundity and estimated population growth were similar under all conditions tested. By contrast, *Ae. aegypti* life history traits were reduced greatly by interspecific interactions (Fig. 1). Resource competition among larvae appeared to be the predominant mode of interaction

in these experiments as limited diet negatively affected pupation time, λ -values, survivorship and fecundity in both species. However, the lack of resources had much more drastic effects on *Ae. aegypti* as cohorts were projected to decline ($\lambda < 1$) under the limited diet condition, whereas for *Ae. albopictus*, although the λ -value decreased, an increase in the cohort was still expected ($\lambda > 1$). In our experiment, *Ae. albopictus* also grew better than *Ae. aegypti* under the optimal diet condition as its rate of increase was significantly greater than that of *Ae. aegypti*. The effect of density on *Ae. albopictus* was not evident in this experiment, suggesting that this species can tolerate higher densities. By contrast, for *Ae. aegypti*, increasing densities in single-species treatments affected fecundity and λ negatively (but not significantly for the latter). At the highest density, the population was projected to decline as most females were unable to oviposit, which suggests that an effect of density becomes evident at a density of about 60 individuals in the context of our experimental design. In the literature, *Ae. aegypti* populations are more often impacted by density dependence than are *Ae. albopictus* populations (Moore *et al.*, 1969; Juliano, 1998; Braks *et al.*, 2004; Murrell & Juliano, 2008). As density had an effect in *Ae. aegypti* under the optimal diet condition, it appears that this did not result solely from exploitation competition. Such effects of competition may reflect an increase in the frequency of physical contact among individuals (Bedhomme *et al.*, 2005) or the toxic effects of waste metabolites (e.g. ammonia) produced by conspecifics at high density (Bedhomme *et al.*, 2005). These metabolites may negatively affect the fitness of *Ae. aegypti* by increasing developmental time, and reducing adult longevity and wing length (Bedhomme *et al.*, 2005), as in our study. The sex ratio (assumed to be 50% male in the wild population) was the only life history trait to be affected in *Ae. albopictus* and not in *Ae. aegypti* under the conditions tested. The sex ratio was female-biased under the limited diet condition, in which males died first. Under the optimal diet condition within a high density of conspecifics, the sex ratio of *Ae. albopictus* was male-biased. These larval laboratory rearing conditions allow the number of males to be maximized and therefore may be advantageous in the rearing of insects for use in sterile insect technique-based programmes.

The co-occurrence of these species did not affect *Ae. albopictus* populations except in terms of female wing length under the limited diet condition. Co-occurrence mainly affected

Ae. aegypti population growth in the limited diet condition, in which no growth was projected in the presence of *Ae. albopictus*. In very limited resource conditions, co-occurrence was seriously harmful to *Ae. aegypti*. The scarcity of *Ae. aegypti* in the field on Reunion Island may reflect this species' poor resistance to unfavourable conditions, including high population density (as a result of density dependence) and interactions with *Ae. albopictus* at low per capita resource availability.

Aedes aegypti has not disappeared from Reunion Island, despite its apparent disadvantage in competition with *Ae. albopictus*, which raises questions about how it persists. It may be that *Ae. aegypti* is currently subject to a process of exclusion from the island, but the process may require more time to complete. Alternatively, behavioural differences (Kesavaraju *et al.*, 2007) or some as yet untested environmental factors may reverse the competitive superiority in local areas, resulting in the island-wide coexistence of these species (Daugherty *et al.*, 2000; Lounibos *et al.*, 2002; Juliano, 2009; Leisham & Juliano, 2009; Costanzo *et al.*, 2011). This scenario may account for the persistence of *Ae. aegypti* in some isolated areas after the arrival of *Ae. albopictus*. For example, drought may contribute to co-occurrence and modify interactions between *Ae. aegypti* and *Ae. albopictus* (Sota & Mogi, 1992; Costanzo *et al.*, 2005). Drought may reverse competitive advantage, allowing *Ae. aegypti* to transiently outcompete *Ae. albopictus* (Costanzo *et al.*, 2005). The fact that *Ae. aegypti* lays bigger and more desiccation-resistant eggs may give it an advantage over *Ae. albopictus* in dry conditions as a positive correlation between egg size and egg survival time has been demonstrated (Sota & Mogi, 1992). In drier environments, *Ae. albopictus* eggs were reported to suffer greater mortality than *Ae. aegypti* eggs (Sota & Mogi, 1992; Juliano *et al.*, 2002; Costanzo *et al.*, 2005). *Aedes aegypti* is also better adapted to life under dry conditions as its immature stages develop more rapidly in comparison with those of *Ae. albopictus*. In dry areas, larval habitats are temporary and water can evaporate rapidly during the hot season; fast developers are thus more likely to succeed under these conditions. The life history traits of the *Ae. aegypti* strain present on Reunion Island suggest better adaptation to dry conditions (i.e. large egg size and shorter development time than *Ae. albopictus*). Indeed, *Ae. aegypti* occurs only on the drier coast (Bagny *et al.*, 2009), where succession in dry and wet periods may give it an advantage. Therefore, populations of *Ae. aegypti* may markedly increase after long periods of dryness when larval habitats are filled with water, and the fluctuation in rainfall in western gullies of the island may contribute to the persistence of this species there. With the exception of the driest coast, all of the Reunion Island ecosystems are hospitable to *Ae. albopictus* in terms of lack of desiccation stress and thus this mosquito would seem likely to outcompete *Ae. aegypti*. Further investigations are needed to evaluate the true role of drought in the persistence of *Ae. aegypti* on the island.

Based on the estimated finite rate of increase (λ), survivorship and estimated fecundity in the conditions tested, of the two species, *Ae. albopictus* is better adapted for the maintenance of positive population growth at a lower per capita resource

availability, at higher densities and colder temperatures. *Aedes albopictus* optimizes the traits of both a good colonizer and a good competitor, whereas the trade-off between these traits may limit the expansion of another ecologically similar species such as *Ae. aegypti*. Reunion Island represents an area where the establishment and expansion of *Ae. albopictus* may have been facilitated by its ecological plasticity in one way but also by its high ability to outcompete the ecologically closest species in different ecological conditions.

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