

Population and Community Ecology

Larval Competition Between *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae) in Argentina: Coexistence and Implications in the Distribution of the Asian Tiger Mosquito

Arturo Andrés Lizuain,^{1,7,✉} Lucia Maffey,^{2,3} Maximiliano Garzón,^{2,3} Marina Leporace,⁴
✉ Danny Soto,⁵ Paula Diaz,⁵ Oscar Daniel Salomón,^{2,5,✉} María Soledad Santini,^{2,6} and
Nicolás Schweigmann^{2,3}

¹Centro Nacional de Diagnóstico e Investigación en Endemo-epidemias (CeNDIE)-ANLIS, Malbrán-Ministerio de Salud de la Nación, Buenos Aires, Argentina, ²Consejo Nacional de Investigaciones Científicas y Técnicas (CONICET), Buenos Aires, Argentina, ³Grupo de Estudios de Mosquitos. Dto. de Ecología, Genética y Evolución, FCEN, UBA e Instituto de Ecología, Genética y Evolución de Buenos Aires (UBA-CONICET), Buenos Aires, Argentina, ⁴Instituto Universitario de Ciencias de la Salud, Fundación H. A. Barceló, Laboratorio de Control de Vectores Entomológicos de Importancia Sanitaria (LaCVEIS), Santo Tomé, Corrientes, Argentina, ⁵Instituto Nacional de Medicina Tropical (INMeT)-ANLIS, Malbrán-Ministerio de Salud de la Nación, Puerto Iguazú, Misiones, Argentina, ⁶Instituto Nacional de Parasitología (INP)-ANLIS, Malbrán-Ministerio de Salud de la Nación, Buenos Aires, Argentina, and ⁷Corresponding author, e-mail: arlizuain@gmail.com

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Abstract

Aedes aegypti (Linnaeus) and *Aedes albopictus* (Skuse) are worldwide vectors of dengue and yellow fever viruses. These species coexist in many countries and the biotic interactions between them can influence their abundances and distributions. In Argentina, *Ae. aegypti* is widely distributed in the north and center regions of the country, with temperate and subtropical climate, while both are sympatric only in the northeastern area of the subtropical region. Interspecific and intraspecific larval competition for food was evaluated to assess if their interaction influences on patterns of abundance and distribution. Finite rates of increase and survivorship for each species were estimated and the effects of mosquito density ratio and detritus availability were determined. The Lambda (λ') index of population performance of both showed there is no competitive exclusion pattern. However, survival of *Ae. albopictus* was negatively affected by the presence of *Ae. aegypti*. These results suggest one possible explanation for the codominance pattern of both species display in rural regions of the southernmost distribution of *Ae. albopictus* in South America. They also show *Ae. aegypti* as a potential biotic barrier for the expansion of *Ae. albopictus* as was reported in regions of the United States.

Key words: invasive species, vector ecology, mosquito

The worldwide spread of epidemic dengue virus, together with the reemergence of Zika, yellow fever, and chikungunya, have highlighted the significant health burden of arboviruses and the need to take urgent action against them (Wilder-Smith et al. 2017). *Aedes aegypti* (Linnaeus) and *Aedes albopictus* (Skuse), the Asian tiger mosquito, are the main vectors of these pathogens in urban and peri-urban environments (Chuchuy et al. 2019, Yang et al. 2021). Both species

are capable of extensive dispersion, which allowed them to colonize many regions outside their native range (Lounibos 2002). *Ae. aegypti* is originated in tropical Africa and colonized America at the beginning of the 16th century, probably transported in slave-trading ships (Vezzani and Carbajo 2008). In the mid-1980s, *Ae. albopictus* populations originally from Japan colonized North America (Spranger and Wuithiranyagool 1986, Birungi and Munstermann

2002), whereas tropical populations from Asia supposedly colonized South America (Forattini 1986, Birungi and Munstermann 2002). As a consequence of continuous invasion processes by both species, their current global distributions overlap significantly (Braks et al. 2003, Tsuda et al. 2006) with more than 3 billion people living in *Aedes* (Meigen) infested regions (Wilder-Smith et al. 2017).

Both species share a similar ecological niche using small artificial containers to lay their eggs, which later hatch into aquatic larval stages that compete for space and food (Paton and Bonsall 2019). Early introduction of *Ae. aegypti* in Asia caused an apparent displacement of native *Ae. albopictus* in large urban centers (Rudnick 1965, Gilotra et al. 1967) whereas, more recently, *Ae. albopictus* successfully displaced *Ae. aegypti* in Florida and Texas, Southern USA (O'Meara et al. 1995). For this reason, interspecific competition for food between *Ae. aegypti* and *Ae. albopictus* larvae has been widely addressed, both in the field and under laboratory conditions (Juliano 2009, 2010). In the United States, studies established a competitive advantage of the Asian tiger mosquito over *Ae. aegypti* (Black et al. 1989, Barrera 1996, Juliano 1998, Daugherty et al. 2000, Braks et al. 2004). However, these results did not explain the coexistence patterns observed in many areas (Rey et al. 2006, Rey and Lounibos 2015). Further experiments evidenced that the competitive exclusion of *Ae. aegypti* by *Ae. albopictus* was context-dependent and heavily relied on the type of food (Daugherty et al. 2000, Murrell & Juliano 2008, Juliano 2009, 2010, Reiskind et al. 2012), seasonal variations in climate (Camara et al. 2016), and population origin (Leisnham et al. 2009, Leisnham and Juliano 2010).

Some authors have proposed that these species display spatial and environmental segregation, with *Ae. aegypti* usually thriving in

urban landscapes and *Ae. albopictus* preferring suburban areas with higher vegetation cover (Braks et al. 2004, Rey et al. 2006, Tsuda et al. 2006, Honório et al. 2009, Reiskind and Lounibos 2013, Heinisch et al. 2019). This pattern could be explained by differential survival rates of eggs and adult specimens and direct larval competition. *Ae. albopictus* eggs are less resistant than those of *Ae. aegypti* to higher temperatures and lower relative humidity, conditions usually associated with urban environments (Sota and Mogi 1992, Mogi et al. 1996, Juliano et al. 2002). At the same time, *Ae. albopictus* prevails in rural and suburban areas (Braks et al. 2003, Rey et al. 2006, Tsuda et al. 2006, Honorio et al. 2009, Reiskind and Lounibos 2013, Heinisch et al. 2019) due to the competitive advantage of its larval stages over *Ae. aegypti* (Juliano 2009, 2010) and the occurrence of reproductive interference (satyrization) (Bargielowski et al. 2015).

In Argentina, the patterns of abundance and distribution of both species differ from those recorded in the United States. In the latter, *Ae. aegypti* has a limited distribution, whereas the Asian tiger mosquito presents an extensive distribution that includes both subtropical and temperate regions with a northern limit corresponding to an isocline of -5°C of mean daily temperature in January (Nawrocki and Hawley 1987). On the contrary, in Argentina, *Ae. aegypti* is widely distributed in urban environments of subtropical regions and displays an ongoing expansion into colder temperate areas (Fig. 1a) (Vezzani and Carbajo 2008, Rubio et al. 2020). On the other hand, *Ae. albopictus* is found only in the subtropical region of Misiones and Corrientes provinces (Fig. 1a and b). This bounded distribution has been regarded as a limited expansion of tropical Brazilian population (Lizuain et al. 2019, Goenaga et al. 2020). Regarding abundance, *Ae. aegypti* is dominant in urban environments and

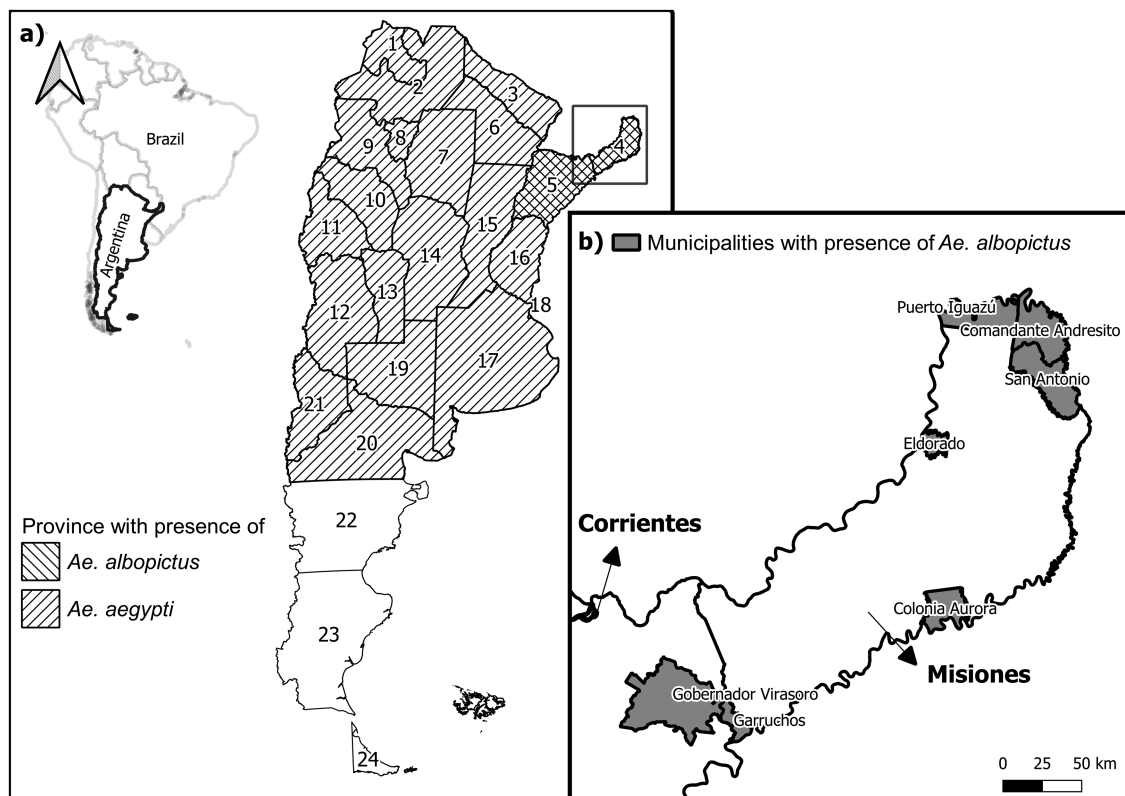


Fig. 1. Provinces with presence of *Ae. albopictus* and *Ae. aegypti* in Argentina (a). Municipalities of Corrientes and Misiones with presence of *Ae. albopictus* (b). Provinces: Jujuy (1), Salta (2), Formosa (3), Misiones (4), Corrientes (5), Chaco (6), Santiago del Estero (7), Tucumán (8), Catamarca (9), La Rioja (10), San Juan (11), Mendoza (12), San Luis (13), Córdoba (14), Santa Fe (15), Entre Ríos (16), Buenos Aires (17), Ciudad Autónoma de Buenos Aires (18), La Pampa (19), Rio Negro (20), Neuquén (21), Chubut (22), Santa Cruz (23), Tierra del Fuego (24).

both species show a pattern of codominance in rural environments (Schweigmann et al. 2004, Espinosa et al. 2012, Lizuain et al. 2019, Faraone et al. 2021).

In this article, we assessed the competitive interaction for food between *Ae. albopictus* larvae from the most southern population found currently in Argentina and local populations of *Ae. aegypti*. The aim of these experiments was to determine if interspecific interactions at larval stage modulate the abundance and distribution patterns for each species. In particular, we sought to determine if the ability of local populations of *Ae. albopictus* to expand to temperate regions might be slowed or impeded by the presence of *Ae. aegypti*. We use an experimental design that allows comparison with studies of other countries, such as the United States (Juliano 1998, Murrell and Juliano 2008) and Brazil (Braks et al. 2004).

Materials and Methods

Sample Collection and Mosquito Rearing

Aedes aegypti and *Ae. albopictus* larvae and pupae were collected from 40 households in Colonia Aurora (27° 28' 29" S, 54° 31' 28" W) during January 2019. Colonia Aurora is a small rural village located in the Province of Misiones. This town was selected based on previous entomological surveys that showed that, up to date, Colonia Aurora is the only Argentinean location where *Ae. albopictus* is well established and presents similar abundances than those of *Ae. aegypti* (Lizuain et al. 2019, Garzón et al. 2020).

To prevent accidental dispersion of *Aedes* adult specimens in other areas, all laboratory assays were conducted in the facilities of the Instituto Nacional de Medicina Tropical (INMeT-ANLIS Malbrán) located in Puerto Iguazú city (province of Misiones), where the natural presence of *Ae. albopictus* was already reported (Espinosa et al. 2012).

Immature stages were placed in acrylic containers with 100 ml of distilled water and reared under standard controlled laboratory conditions (27°C and a photoperiod of 14:10 (L:D) h). Larvae were fed with a 10% yeast solution and separated into individual containers once they reached pupal stage. After emergence, taxonomic determination was performed using a stereoscopic microscope and adult specimens were separated by species in cages (30 cm × 30 cm × 30 cm). Adult mosquitoes were fed ad libitum with a 10% sugar solution and allowed to mate. Three days after copulation, females were provided with blood meal and oviposition substrate as previously described (Garzón et al. 2020). Eggs were collected daily and observed under a stereoscopic microscope to assess their condition. F1 viable eggs were stored under laboratory conditions (27°C, 75% RH, and a photoperiod of 14:10 (L:D) h) until the beginning of the assay.

Experimental Design

Experiments were conducted between February and April of 2019. In order to better emulate field conditions, larvae were maintained under environmental conditions (maximum and minimum mean daily temperatures of 21.38°C and 29.45°C, respectively). The food of mosquito larvae (based on microorganisms that generally come from the detritus of plants and other insects) consisted of fallen avocado leaves collected in the study area, sundried, chopped, and weighted as previously reported (Braks et al. 2004). F1 larvae were placed in artificial containers (AC: 500 ml plastic containers, 8.5 cm high, 9.5 cm diameter). Interspecific competition was assessed by monitoring larval development under variable conditions of mosquito density, species ratio, and

food availability. This design yielded six combinations of *Ae. albopictus*:*Ae. aegypti* (10:0, 40:0, 30:10, 10:30, 0:40, and 0:10) and two food levels (0.25/0.50 g). Each combination was replicated four times, providing a total of 48 containers (Table 1). In all cases, avocado leaves were placed in the plastic containers carrying 250 ml of distilled water and covered with tulle fabric. Water levels were assessed daily and refilled when necessary. After mosquitoes reached pupal stage, they were removed from the container and placed individually until emergence. Adult specimens were frozen and species, sex, pupation, and emergence dates were recorded.

Data Analysis

Developmental time (DT) was estimated as the number of days from first instar to adult. Size of adult specimens was determined by removing both wings and measuring wing sizes under a stereoscopic lens as described in previous studies (Braks et al. 2004). We defined survival of immature stages as the proportion of individuals of the same species that reached adulthood. Finally, we employed a composite index of population performance λ' , as previously described (Juliano 1998). Briefly, this index is based on r' ($\lambda' = \exp[r']$), which estimates the realized per capita rate of population change for each experimental treatment (Livdahl and Sugihara 1984). When $\lambda' = 1$, mosquito cohorts remain constant, $\lambda' > 1$ entails positive population growth whereas $\lambda' < 1$ accounts for negative growth. Finally, $\lambda' = 0$ implies that cohort only reached the first generation. λ' was therefore calculated for each experimental treatment as follows:

$$\lambda' = \exp \left[\frac{\ln \left[\left(\frac{1}{N_0} \right) \sum_X A_X f(\omega_X) \right]}{D + \left[\frac{\sum_X x A_X f(\omega_X)}{\sum_X A_X f(\omega_X)} \right]} \right] \quad [1]$$

where N_0 is the initial number of females in a cohort (assuming a 1:1 sex ratio), A_X is the number of females that emerged on day x , ω_x is an estimator of female size on day x , $f(\omega_x)$ represents a function that associates fecundity and female size, and D is the number of days that an emerged female requires to copulate, feed on a blood meal, and lay eggs (Braks et al. 2004). Previous estimations have yielded D values of 12 and 14 d for *Ae. aegypti* and *Ae. albopictus*, respectively (Juliano 1998). Size-fecundity relationships were estimated as follows.

For *Ae. aegypti* (Breigel 1990):

$$f(\omega_x) = 2.50\omega_x^3 - 8.616 \quad [2]$$

$$r^2 = 0.875, N = 206, P < 0.001$$

where ω_x is wing length (in mm) on day x , elevated to the third power.

For *Ae. albopictus* (Lounibos et al. 2002):

$$f(\omega_x) = 78.02\omega_x - 121.24 \quad [3]$$

Table 1. Summary of the number of artificial containers (AC) for each treatment combination (ratio of mosquito densities) and food (detritus availability)

	Treatment (mosquito density ratio)					
	<i>Ae. albopictus</i> (ALB): <i>Ae. aegypti</i> (AEG)					
	10:0	40:0	30:10	10:30	0:40	0:10
Food (availability)	0.25 g	4	4	4	4	4
	0.50 g	4	4	4	4	4

$$r^2 = 0.713, N = 91, P < 0.001$$

where w_x is wing length (in mm) on day x .

Pupal specimens that did not reach adulthood (8.01%) were included in the analysis as emerging adults. Sex and species determination was assessed by observing morphological trait (Braks et al. 2004).

To evaluate the effects of treatment, food, sex, and their interactions on developmental time and adult size, Generalized Linear Mixed Models (GLMM) with AC as random factors were performed. To assess whether the survival of each species is affected by treatments (combinations of *Ae. albopictus*:*Ae. aegypti*), food (availability), and its interaction, Generalized Linear Models (GLM) were performed. Developmental time analyses were performed with R package lme4 (Bates et al. 2015) whereas adult size and survival were studied using package glmmTMB (Brooks et al. 2017).

Forward selection method was employed to choose the most explicative variables (Quinn and Keough 2002). Selected models included all explicative variables with significant estimators and lowest values for deviance and variance inflation factor (Davis 1989). When necessary, Tukey's test was applied to compare means between treatments. In all cases, model assumptions and residual analysis were conducted using DHARMA package as implemented in R (Hartig 2020).

No data transformation allowed us to comply with normality and homoscedasticity assumptions, therefore the analysis of λ' for both species was conducted using ANOVAs with permutation (Anderson and Robinson 2001). Since sum squares values were similar for ANOVAs and permutation ANOVAs, differences between treatments were evaluated using Tukey tests (Braks et al. 2004). Ninety-five percent confidence intervals for means were determined using Bootstrap method and evaluated for inclusion of $\lambda' = 0$ and $\lambda' = 1.0$ (Braks et al. 2004).

Results

Developmental Time (DT)

For both species, developmental time was conditioned by sex (*Ae. albopictus*: $\chi^2 = 18.34$, FD = 1, $p = 1.85 \times 10^{-5}$; *Ae. aegypti*: $\chi^2 = 15.88$, FD = 1, $p = 6.75 \times 10^{-5}$) (Table 2) with males developing faster than females (Fig. 2a–d). Density treatments also affected DT in *Ae. albopictus* ($\chi^2 = 56.91$, FD = 3, $p = 2.69 \times 10^{-12}$) and

Ae. aegypti ($\chi^2 = 34.04$, FD = 3, $p = 1.94 \times 10^{-7}$) (Table 2). Median time to adulthood for *Ae. albopictus* increased with density (10:0 vs 40:0) but also when coexisting with different densities of *Ae. aegypti* (30:10; 10:30) (Fig. 2a). For *Ae. aegypti*, DT increased in treatments with higher density levels for the species, regardless of *Ae. albopictus* density (Fig. 2d).

Adult Size

Median wing length in *Ae. albopictus* was significantly affected by sex ($\chi^2 = 237.13$, FD = 1, $p < 2.2 \times 10^{-16}$), food ($\chi^2 = 7.58$, FD = 1, $p = 5.91 \times 10^{-3}$), and density treatment ($\chi^2 = 7.58$, FD = 1, $p = 5.91 \times 10^{-3}$) (Table 3). Males were significantly smaller than females, whereas individuals raised under low food availability showed smaller wing lengths than those raised with high availability (Fig. 2c). Finally, significant differences were found between the lowest and the highest density treatments (10:0 vs 40:0) (Fig. 2b).

For *Ae. aegypti*, wing length was conditioned by sex ($\chi^2 = 157.55$, FD = 1, $p < 2.2 \times 10^{-16}$) (Table 3), with males presenting smaller lengths than females (Fig. 2e), following the same trend as *Ae. albopictus*. Density treatments also affected adult size ($\chi^2 = 18.79$, FD = 3, $p = 3.02 \times 10^{-4}$), with specimens from the 30:10 treatment displaying significantly lower values than those of the 0:40 and 10:30 treatments (Fig. 2c).

Survival

Food significantly affected survival in *Ae. albopictus* ($\chi^2 = 96.89$, FD = 1, $p < 2.2 \times 10^{-16}$) and *Ae. aegypti* ($\chi^2 = 59.89$, FD = 1, $p = 9.99 \times 10^{-15}$) (Table 4). Survival decreased for all mosquitoes that received 0.25 g of avocado leaves with respect to those receiving 0.5 g, regardless of the species abundance ratio (Fig. 3a and c). Mosquito density (treatment) also conditioned survival in *Ae. albopictus* ($\chi^2 = 46.73$, FD = 3, $p = 3.95 \times 10^{-7}$) and *Ae. aegypti* ($\chi^2 = 42.83$, FD = 3, $p = 2.67 \times 10^{-9}$). *Ae. albopictus* presented higher survival values when present in low abundances and without *Ae. aegypti* (10:0) (Fig. 3a), whereas *Ae. aegypti* displayed higher survival under low densities whether *Ae. albopictus* was present or not (Fig. 3c).

Estimate Finite Rate of Increase (λ')

For *Ae. albopictus*, using 0.5 g of avocado leaves, means of λ' were >1 and 95% confidence intervals did not include 1 when *Ae.*

Table 2. Selected GLMM for *Ae. albopictus* and *Ae. aegypti* development time

Development time						
Model: Development ~ gender + treatment						
Gamma distribution (link function = "inverse")						
	<i>Ae. aegypti</i>			<i>Ae. aegypti</i>		
	Coefficient	SE	p-Value	Coefficient	SE	p-Value
Intercept	0.059	0.005	<2.00e-16	0.080	0.008	<2E-16
Sex.Male	0.007	0.001	5.27E-05	0.011	0.003	5.32E-04
TREAT.10:30	-0.038	0.008	1.42E-06	-0.047	0.013	2.64E-04
TREAT.30:10	-0.038	0.007	3.44E-07	-0.053	0.010	7.54E-08
TREAT.40:0	-0.022	0.007	2.18E-03	-0.039	0.010	1.76E-04
TE variance:	6.29E-05			5.87E-05		
Residual deviance:	1305.8			625.2		
df residual:	164			82		

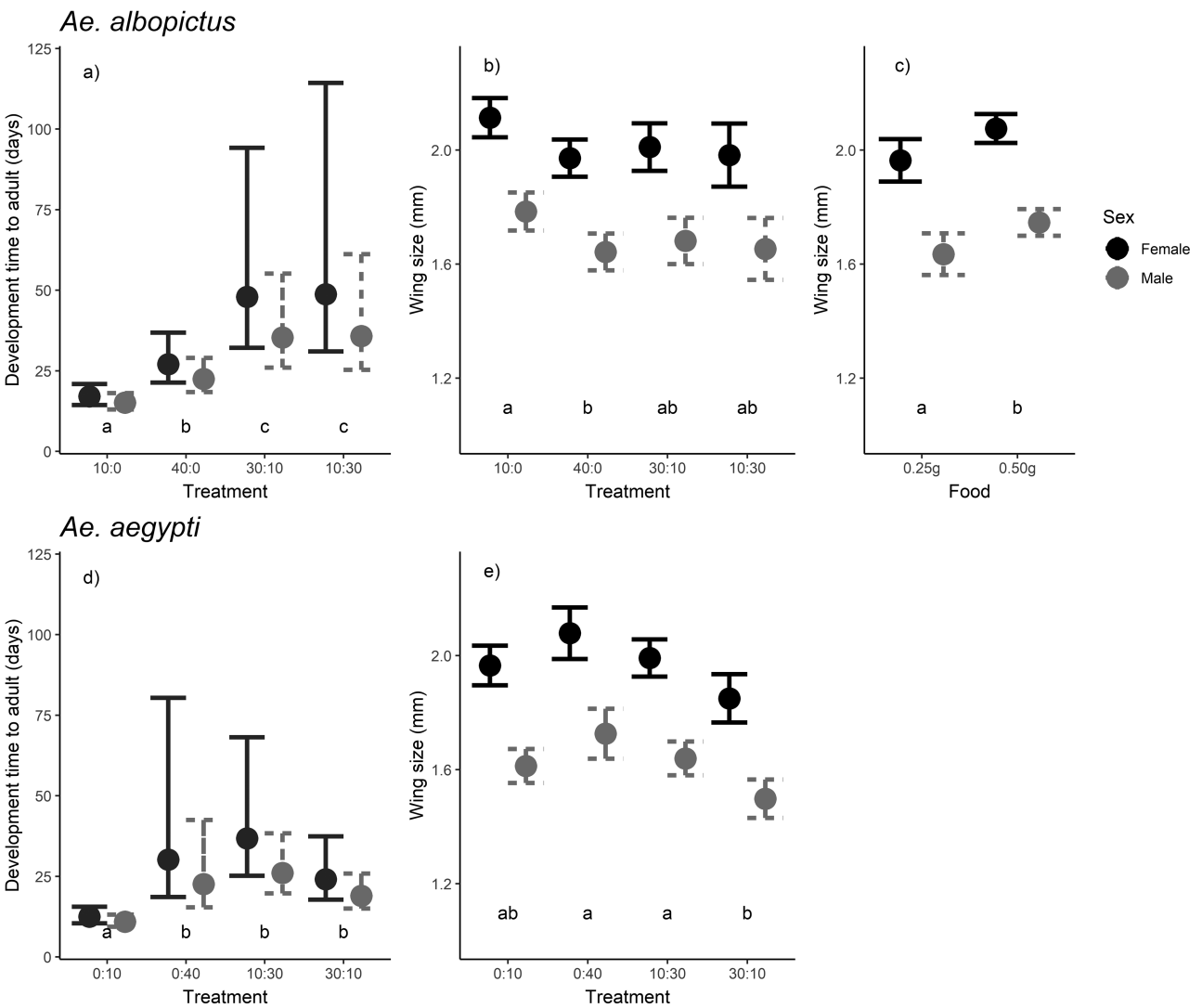


Fig. 2. Developmental time to adulthood (DT, in days) and wing size (mm) for *Ae. albopictus* and *Ae. aegypti* analysed by sex (males vs females) and density treatments. (a) and (d): DT according to ALB:AEG treatment type (0:10, 0:40, 10:30, 30:10, 40:0, 10:0) and sex. (b), (c), and (e) Wing size according to treatment and sex. Circles represent estimated values for each selected model, whereas lines depict 95% confidence intervals. Treatments with different letters presented significant differences according to Tukey's test results ($p < 0.05$).

Table 3. Selected GLMM for *Ae. albopictus* and *Ae. aegypti* wing size

Wing size							
<i>Ae. albopictus</i>				<i>Ae. aegypti</i>			
Model: Wing size ~ gender + treatment + food Gaussian distribution (link function = "identity")				Model: Wing size ~ gender + treatment Gaussian distribution (link function = "identity")			
	Coefficient	SE	p-Value		Coefficient	SE	p-Value
Intercept	2.170	0.038	<2E-16	Intercept	1.965	0.035	<2e-16
Sex.Male	-0.329	0.021	<2E-16	Sex.Male	-0.352	0.028	<2e-16
TREAT.10:30	-0.131	0.062	0.036	TREAT.0:40	0.113	0.051	0.027
TREAT.30:10	-0.103	0.051	0.042	TREAT.10:30	0.026	0.040	0.507
TREAT.40:0	-0.142	0.044	0.001	TREAT.30:10	-0.115	0.045	0.010
Food.0,25g	-0.111	0.040	0.006				
TE variance: 4.506E-3				TE variance: 1.231E-3			
Residual deviance: -176.3				Residual deviance: -114.1			
df residual: 138				df residual: 67			

Table 4. Selected GLM for *Ae. albopictus* and *Ae. aegypti* survival

Survival						
Model: Survival ~ food + treatment Binomial distribution (link function = “logit”)						
	<i>Ae. albopictus</i>			<i>Ae. aegypti</i>		
	Coefficient	SE	<i>p</i> -Value	Coefficient	SE	<i>p</i> -Value
Intercept	1.051	0.283	2.07E-04	1.051	0.283	2.07E-04
Food.0,25 g	-2.102	0.246	2.00E-16	-2.102	0.246	2.00E-16
TREAT.10:30	-1.997	0.417	1.64E-06	-1.997	0.417	1.64E-06
TREAT.30:10	-2.102	0.328	1.51E-10	-2.102	0.328	1.51E-10
TREAT.40:0	-1.667	0.304	4.07E-08	-1.667	0.304	4.07E-08
Residual deviance: 48.21 df residual: 27				Residual deviance: 74.99 df residual: 27		

aegypti was not present, suggesting that cohorts would increase regardless of their initial abundance (ALB:AEG,10:0 or 40:0). When *Ae. aegypti* was present (30:10 or 10:30), *Ae. albopictus* displayed mean values < 1 of λ' although, in this case, 95% confidence intervals did include 1. With 0.25 g of leaves, means of λ' were < 1 in the absence of *Ae. aegypti* (10:0 or 40:0), and confidence intervals included 1. Finally, with 0.25 g of leaves and when *Ae. aegypti* was also present, mean λ' for *Ae. albopictus* were lower than 1, and confidence intervals were lower than 1 for both density treatments (30:10 or 10:30). Finite rate of increase of *Ae. albopictus* was affected by food but also by mosquito density (treatment) (Table 5). Lower availability of food significantly decreased λ' , whereas the highest λ' values were achieved when *Ae. albopictus* was present in lower densities and without *Ae. aegypti* (10:0, Fig. 3b). No significant interaction between treatments was detected (Table 5).

For *Ae. aegypti*, 95% confidence intervals of λ' included $\lambda' = 1$ for all experimental treatments with high availability of food (0.5 g). When 0.25 g of leaves were supplied, all values of λ' were <1. Finite rate of increase of *Ae. aegypti* was only significantly affected by food availability (Table 5). In this case, λ' was significantly higher with 0.5 g of avocado leaves, regardless of mosquito density (Fig. 3d).

Discussion

In this experiment, we analyzed interspecific and intraspecific competition in *Ae. albopictus* and *Ae. aegypti* populations from the north-eastern region of Argentina. In treatments with high availability of food, finite rate of increase of *Ae. aegypti* presented low values under conditions of high conspecific abundance, while it increased in the presence of Asian tiger mosquito. These differences between intraspecific and interspecific competition also were detected in *Ae. Aegypti*'s survival, being significantly lower in treatments 0:40. On the other hand, finite rate of increase and survival of *Ae. albopictus* were negatively conditioned by the presence of *Ae. aegypti*. These results would imply that, for Argentinean populations, there is no competitive exclusion pattern of *Ae. aegypti* by *Ae. albopictus*, as previously reported in Brazil (Braks et al. 2004, Camara et al. 2016) and in the United States (Juliano 1998); and this could explain the patterns of codominance observed in rural regions of Argentina (Lizuain et al. 2019). Also, the presence of *Ae. aegypti* could be affecting local Asian tiger mosquito, as it has been described in some regions of the United States where *Ae. aegypti* is considered a biotic barrier for the expansion of *Ae. albopictus* (Leisnham and Juliano 2010).

Other authors have proposed that competitive exclusion patterns are context-dependent and vary according to the quality of available food, geographic variations in competitive performance and presence of predators or parasites (Juliano 2009, Leisnham et al. 2009, Juliano 2010, Leisnham and Juliano 2010). In this article, we followed the guidelines proposed by Braks (et al. 2004) regarding experimental design, food type, and statistical analysis. Differences in the species competitive performance between the two studies could be explained by divergent population dynamics.

It has been previously stated that North American populations of *Ae. albopictus* are more related to temperate populations from Japan, which could explain their ability to induce diapause in eggs to anticipate unfavorable environmental conditions. On the other hand, the absence of photoperiodic-induced diapause in Brazilian populations of *Ae. albopictus* suggests a tropical origin, probably from Southeast Asia (Hawley et al. 1987, Lounibos et al. 2003, Kotsakiozi et al. 2017). Although no genetic analyses have included *Ae. albopictus* specimens from Argentina, it is currently assumed that Argentinean populations share the same origin as the Brazilian ones, mostly based on their geographic closeness, and that the former reports from Argentina were in localities found on the bi-national border. Even if a common origin was confirmed, in this experiment we used one of the most southern populations of the Asian tiger mosquito, whereas previous studies employed specimens from Rio de Janeiro (Brazil) and Florida (USA) (Juliano 1998, Braks et al. 2004). Significant differences on variability and genetic structure have been detected at continental level, with strong population divergence at this scale (Birungi and Munstermann 2002, Bracco et al. 2007, Kotsakiozi et al. 2017). These discrepancies could also include life history traits and interspecific competitive behavior, as it occurs in the United States (Leisnham et al. 2009, Leisnham and Juliano 2010), where it has been observed that a better performance of *Ae. aegypti* in some regions is considered a biotic barrier for the spread of Asian tiger mosquito (Leisnham and Juliano 2010).

Some feature of our experiment differed from those of Juliano (1998) and Braks et al. (2004), including container and food type and environmental conditions. In our experiment, we used 500 ml plastic containers with 250 ml of water with avocado leaves as food. Braks et al. (2004) used similar containers and food, while Juliano (1998) conducted his field experiment with tires and oak leaves (0 and 1 g). According to Braks et al. (2004), the type of container did not affect the competitive result between *Ae. albopictus* and *Ae. aegypti* when they compare their experience in Brazil with the one in the United States (Juliano 1998). This suggests that changes in

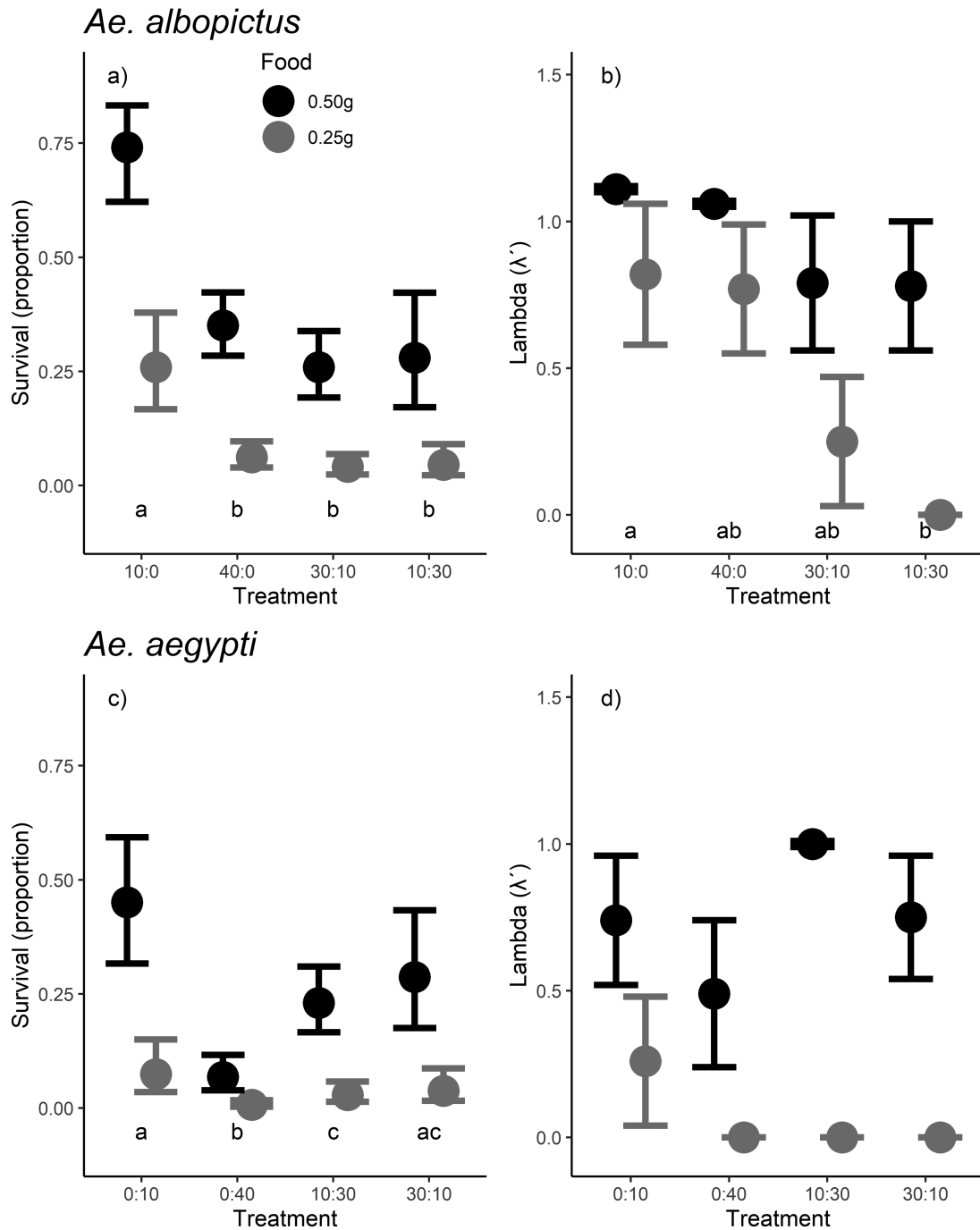


Fig. 3. Estimated finite rate of increase (λ') and survival (proportion) of *Ae. albopictus* and *Ae. aegypti* for each treatment combination (combination *Ae. albopictus*: *Ae. aegypti*) and quantity of food (0.25 g and 0.50 g). (a) and (c): Dots indicate mean of λ' and lines, standard error. In 0.50 g_10:0 and 0.50 g_40:0 treatments of *Ae. albopictus*, the standard deviation is not visualized by the size of the point. In 0.25 g_10:30 treatments of *Ae. albopictus* and 0.25 g_0:40, 0.25 g_10:30, 0.25 g_30:10 of *Ae. aegypti*, no female emergence was recorded. (b) and (d): Points indicate estimated survival values for each selected model and lines, 95% confidence interval. Treatments that share the same letter are not significantly different in the Tukey's test ($p < 0.05$).

competitive performance are due to population differences, although the type of detritus in Aedes inhabited containers and effect on competitive performance should be addressed.

Effects of food type on competition between *Ae. albopictus* and *Ae. aegypti* are well documented (Juliano 2009, 2010). Barrera (1996) showed that using artificial food rich in protein generated a competitive advantage for *Ae. aegypti*. In other experiments with avocado and oak leaves as resource, a competitive displacement of

Ae. albopictus over *Ae. aegypti* was observed (Juliano 1998, Braks et al. 2004; Murrell and Juliano 2008), while with insect carcasses and grass coexistence was promoted (Murrell and Juliano 2008). Our results didn't show a pattern of competitive exclusion, despite the use of avocado leaves. Therefore, it contributes to the idea that changes in competitive performance are due to population factors.

As in ours, Juliano (1998) and Braks et al. (2004) carried out their experiments at room temperature. In the first article, the average

Table 5. ANOVA with permutations of λ' in *Ae. albopictus* and *Ae. aegypti* under different conditions of detritus availability (DA), Mosquito Density Ratios (MDR), and interactions between them (DA:MDR)

	<i>Ae. albopictus</i>			<i>Ae. aegypti</i>		
	FD	SS	<i>p</i>	Gl	SS	<i>p</i>
Food	1	1.796	6E-04	1	3.795	<2e-16
Treatment	3	1.949	0.025	3	0.349	0.232
Food:Treatment	3	0.328	0.553	3	0.341	0.632
Error	24	4.078		24	3.296	

FD, freedom degrees; SS, Sum of Squares; *p*: *p*-value.

ambient temperature was 24.8°C; while in the second, it averaged 27.4°C. Lounibos et al. (2002) showed that for *Ae. albopictus* and *Ae. Aegypti*, a variation between 24 and 30°C does not modify the competitive result of the interaction. As in the other experiment, an average daily temperature of (26.4°C) was included in these ranges, so it could be expected that the result is not influenced by this environmental factor.

Regarding life history traits, there were inter and intraspecific effects for both species. Survivorship of *Ae. albopictus* decreased when mosquito density was high, regardless of the species ratio (40:0, 30:10, or 10:30), suggesting similar effects of interspecific or intraspecific competition on this trait. Our results showed a similar trend to the ones obtained for *Ae. albopictus* populations in Brazil and the United States (Juliano 1998, Braks et al. 2004, Camara et al. 2016). On the other hand, *Ae. aegypti* survivorship was affected by intraspecific factors rather than by interspecific competition. Survivorship rate for 0:40 treatment was the lowest, whereas these values sequentially increased for 10:30 and 30:10 treatments, respectively. No significant differences were detected between 0:10 and 30:10 treatments, indicating that the presence of *Ae. albopictus* larvae did not affect *Ae. aegypti* survivorship. A similar pattern was found in another study with the same species that used pine leaves as detritus (Murrel and Juliano 2008) and in other experiments involving interspecific and intraspecific competition between *Aedes hendersoni* (Cockerell) and *Aedes triseriatus* (say), two mosquito species that breed on tree holes in the United States (Copeland and Craig 1992). The role of intraspecific competition can overcome the effects of interspecific competition because individuals from the same species tend to exploit the same resources in a similar way (Begon et al. 2006). In mosquitoes, larval feeding behavior varies between species (Yee et al. 2004). When food levels are low, *Ae. albopictus* spends more time on the leaves' surface, whereas *Ae. aegypti* is usually found in the container's wall and bottom (Yee et al. 2004). This spatial segregation inside breeding containers could imply a differential use of the same resource and help to explain the predominant effect of intraspecific competition in *Ae. aegypti*.

Unlike previous studies that only used females (Juliano 1998, Braks et al. 2004), we also incorporated males for development time and adult size analyses. As expected, male specimens presented shorter development times and smaller adult size when compared to females. We did not find significant interactions between sex and other variables in any of the models, which suggests that mosquito density and/or food availability affect both females and males alike.

Also, food availability did not affect development time for either species, in contrast to Brazilian populations, where *Ae. albopictus* increased its development time to adult when resources were low (Braks et al. 2004). In Argentinean populations, interspecific

competition caused a delay in *Ae. albopictus* development rate, whereas *Ae. aegypti* showed no significant differences. Regarding adult size, no significant differences were found between treatments, as described in previous studies (Braks et al. 2004), suggesting that neither interspecific nor intraspecific competition affects this variable.

Here, we have shown that *Ae. albopictus* and *Ae. aegypti* populations from northeastern Argentina do not exhibit a pattern of competitive exclusion. Our results could explain the abundance trend observed in the rural environment of Colonia Aurora (Lizuain et al. 2019). In this town, both species have a similar relative abundance, representing 37.1% and 34.3% (respectively) of the specimens collected in artificial breeding sites (Lizuain et al. 2019). Previous studies in Brazil, the United States, and Thailand evidenced a process of environmental segregation between these species: *Ae. aegypti* prevailed in urban areas, whereas *Ae. albopictus* was found in higher abundances in rural areas (Braks et al. 2003, Rey et al. 2006, Tsuda et al. 2006, Reiskind and Lounibos 2013). This type of environment would be more favorable for the survival of eggs and adults of Asian tiger mosquito, which ultimately causes the displacement of *Ae. aegypti* through larval competition and satyriation (Sota and Mogi 1992, Mogi et al. 1996, Reiskind and Lounibos 2013). However, for the population of Argentina, since there is no pattern of competitive exclusion and, possibly, as demonstrated in Brazil, satyriation does not occur either (Honorio et al. 2018), codominance would be observed in rural environments.

Potential distribution studies indicate that *Ae. albopictus* could be found at higher latitudes in Argentina (Benedict et al. 2007; Kremer et al. 2015). However, until now, it was assumed that the Asian tiger mosquito was limited to subtropical regions due to the lack of diapause (Lounibos et al. 2003). Our study is the first to show a potential population divergence in the competitive ability of *Ae. aegypti* in South America that could affect the ongoing invasion process of *Ae. albopictus*. Despite not observing a pattern of competitive exclusion, high abundances of *Ae. aegypti* could affect the survival of the latter. Ecological interactions between the well-established population of *Ae. aegypti* and the Asian tiger mosquito (in small propagules) are likely to reduce its establishment, regulating its population growth and expansion. Competition has generally been invoked as an important process conferring biotic resistance of resident communities to exotic invaders in plants (Levine et al. 2004), but is relatively understudied among insects (Leisnham and Juliano 2010).

These results provide evidence as to why *Ae. albopictus* is found in low abundance and with a limited distribution in Argentina. Although this bounded distribution could be seen as a potential epidemiological advantage, it is important to point out that previous studies also indicate that, for this species, larval competition increases the probability of acquiring arbovirus infections (Alto et al. 2005) and increasing its vectorial capacity (Juliano 2009). So, the competitive effects of *Ae. aegypti* on *Ae. albopictus* could pose a greater public concern that needs to be closely monitored.

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