

# Effects of photoperiod on population performance and sexually dimorphic responses in two major arbovirus mosquito vectors, *Aedes albopictus* and *Aedes aegypti* (Diptera: Culicidae)

K.S. Costanzo\*, R.A. Dahan and D. Radwan

Department of Biology, Canisius College, 2001 Main St., Buffalo, NY, 14208, USA

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**Abstract.** The Asian tiger mosquito, *Aedes albopictus* (Skuse) and the yellow fever mosquito, *Aedes aegypti* (Linnaeus) are medically important species that vector several arboviruses. Globally, populations of both species experience (and are sensitive to) photoperiodic variations. The present study aims to test if photoperiod regimes affect the population performance of *Ae. albopictus* and *Ae. aegypti*. Since mosquitoes have sex-specific strategies to maximize fitness, we also tested the hypothesis that *Ae. albopictus* and *Ae. aegypti* would exhibit differences in the male and female response (sexually dimorphic response) to various photoperiod treatments. We reared cohorts of first instar larvae to adulthood in three photoperiod treatments: short day (10 h light), control (12 h light) and long day (14 h light). We measured and compared survival to adulthood, population growth, development time of males and females, and wing length across treatments. Although we detected no effects of photoperiod on the population performance of both species, we found evidence of a sexual dimorphic response to photoperiod in *Ae. albopictus*, but not in *Ae. aegypti*, with *Ae. albopictus* females being more sensitive to variations in photoperiod. The observed differences between sexes of *Ae. albopictus* are consistent with sex-specific developmental constraints. The absence of a sexually dimorphic response to photoperiod in *Ae. aegypti* can be attributed to different strategies evolved in this species to prepare for unfavourable conditions associated with shorter day length. We discuss the ecological and medical implications of our findings.

**Key words:** *Aedes albopictus*, *Aedes aegypti*, photoperiod, sexual dimorphism

## Introduction

Several insects exhibit phenotypic plastic responses to varying environmental conditions (West-Eberhard, 2003). On both a spatial and temporal scale, mosquitoes encounter variable environmental conditions that can induce changes in individual traits, including development, growth, fecundity, gonotrophic cycles and lifespan,

along with effects on population performance. Since individual to population level changes of mosquitoes can impact disease transmission (Dye, 1986), the effects of the environment on these insects are important, both ecologically and medically. Photoperiod (day length) is an abiotic factor that provides valuable information on seasonal changes and often acts as a cue to induce phenotypic plastic changes in organisms. In several insects, fluctuations in photoperiod can induce changes in behaviour, development and growth, or induce diapause as

\*E-mail: [costanz4@canisius.edu](mailto:costanz4@canisius.edu); [kscosta@gmail.com](mailto:kscosta@gmail.com)

unfavourable conditions approach (Tauber *et al.*, 1985; Nylin and Gotthard, 1998). Specifically, in mosquitoes, photoperiod can alter life history traits and induce diapause in some species (Anderson, 1968; Jordan and Bradshaw, 1978; Hawley *et al.*, 1987; Lanciani and Anderson, 1993; Leisnham *et al.*, 2011; Yee *et al.*, 2012; Costanzo *et al.*, 2015).

The Asian tiger mosquito, *Aedes (Stegomyia) albopictus* (Skuse) and the yellow fever mosquito *Aedes (Stegomyia) aegypti* (Linnaeus) (Diptera: Culicidae) are well-studied species due to their medical importance, as they vector several human pathogens. *Aedes aegypti* is the primary vector for dengue fever, chikungunya, yellow fever and the emergent Zika virus in several regions of the world (Tabachnick, 1991; Hayes, 2009; Paupy *et al.*, 2010; Richards *et al.*, 2012; Vega-Rúa *et al.*, 2014). *Aedes albopictus* also serves as a vector for dengue and chikungunya, and has been implicated as a potential vector for Zika, Ross River, West Nile, La Crosse and Eastern equine encephalitis viruses (Gratz, 2004; Paupy *et al.*, 2010; Rezza, 2012; Richards *et al.*, 2012; Grard *et al.*, 2014; Vega-Rúa *et al.*, 2014). The impact of numerous environmental factors, including temperature, rainfall, larval competition and nutrition on the life history and population dynamics of *Ae. albopictus* and *Ae. aegypti* have been extensively studied (Alto and Juliano, 2001; Costanzo *et al.*, 2005; Alto *et al.*, 2008a; Bevins, 2008; Delatte *et al.*, 2009; Joy *et al.*, 2010; Roiz *et al.*, 2010; Mohammed and Chadee, 2011; Brady *et al.*, 2013; Carrington *et al.*, 2013a, b; Waldock *et al.*, 2013). Despite the importance of photoperiod as a seasonal cue, relatively few studies have investigated the effect of photoperiod regimes on the ecology and life history of these two species (Lounibos *et al.*, 2003; Leisnham *et al.*, 2011; Yee *et al.*, 2012; Costanzo *et al.*, 2015).

*Aedes albopictus* is native to Asia and India (Hawley, 1988), but has been successfully introduced to nearly every continent throughout the world, including North America (Lounibos, 2002). In the United States, *Ae. albopictus* ranges across 36 states, most in the southeast, but populations have been detected as far north as New Jersey, New York and Pennsylvania (Enserink, 2008). Originating from Africa, *Ae. aegypti* is established in many tropical and sub-tropical regions throughout the Americas, the African continent, India and Southeast Asia. In the US, *Ae. aegypti* occupies 23 states (also mainly in the southeast), and is found as far north as Indiana and Kentucky (Darsie and Ward, 2005; Reiter, 2010; Eisen and Moore, 2013). For both species, many populations around the world encounter seasonal fluctuations in photoperiod and can remain active during periods with shorter day lengths, particularly *Ae. aegypti* (Reiskind and

Lounibos, 2013; Tsunoda *et al.*, 2014). *Aedes albopictus* and *Ae. aegypti* both have evolved receptivity to photoperiodic fluctuations, and females have been found to exhibit species-specific responses in life history. For instance, *Ae. albopictus* females emerge at different body sizes across different photoperiod treatments, and under shorter day lengths, produce diapausing eggs. *Aedes aegypti* females cannot produce diapausing eggs and are unable to exhibit plasticity in body size across different photoperiods, but increase blood-feeding activity and live longer as adults under shorter day conditions (Lounibos *et al.*, 2003; Leisnham *et al.*, 2011; Yee *et al.*, 2012; Costanzo *et al.*, 2015).

To date, little is known of how photoperiod may affect population performance (e.g. survival and population growth) in *Ae. albopictus* and *Ae. aegypti*. In addition, most studies have focused on female responses of these two species to photoperiod (Lounibos *et al.*, 2003; Leisnham *et al.*, 2011; Costanzo *et al.*, 2015), since females are the sex that transmits diseases important to human health. However, male responses to environmental factors are also of interest, not only to reach more accurate predictions of the population performance, but to also provide information on if males and females respond differently to environmental variation (sexually dimorphic responses), which is illustrated in several insects (Teder and Tamaru, 2005).

Mosquitoes exhibit sex-based differences in life history traits because males and females achieve maximum fitness through different developmental strategies (Steinwascher, 1982; Kleckner *et al.*, 1995). Females maximize fitness by emerging at a larger size, which increases their fecundity, but they attain this larger size at the expense of a slower developmental rate (Steinwascher, 1982; Briegel, 1990; Lounibos *et al.*, 2002). In contrast, males maximize their fitness by increasing their rate of development with associated costs of a smaller body size. This earlier emergence (protandry) provides more mating opportunities and a greater probability of access to virgin females (Steinwascher, 1982).

Because of these different selective pressures on development and growth between the two sexes, different plastic responses to variable environments may have been selected for in males and females. In *Ae. albopictus* and *Ae. aegypti*, differences in male and female phenotypic responses have been illustrated across varying environmental conditions such as resource levels, temperatures, predator regimes and competitive environments (Juliano, 1998; Bedhomme *et al.*, 2003; Costanzo *et al.*, 2011a; Padmanabha *et al.*, 2011; Wormington and Juliano, 2014). With respect to photoperiod, Yee *et al.* (2012) found that *Ae. albopictus* females

illustrated a stronger response in life history traits to photoperiod and found a greater degree of sexual dimorphism between male and female size and development time when reared in longer day photoperiod treatments. However, the trends in *Ae. albopictus* life history traits across photoperiod studies are inconsistent (Yee *et al.*, 2012; Costanzo *et al.*, 2015), due to varying experimental protocols (e.g. temperature, resources); thus, it is of interest to measure these responses under different environmental conditions. In *Ae. aegypti*, sexual dimorphic responses to photoperiod have yet to be investigated. Since photoperiod is an important seasonal cue that induces phenotypic change in insects, and males and females experience different selective pressures to maximize fitness, it is of interest to determine if males and females respond differently to photoperiod regimes.

In this study, we investigate the effect of photoperiod on population performance (survival and population growth) of both *Ae. albopictus* and *Ae. aegypti*. In addition, we aim to detect if there are any differences in male and female phenotypic responses (developmental rate, body size) to photoperiod in both species. We also compare the performance of both these species across three photoperiod treatments in laboratory experiments.

## Materials and methods

### Experiment I: *Ae. albopictus*

This experiment tested the effects of varying photoperiod regimes on male and female development time and body size, along with population growth and survival to adulthood in *Ae. albopictus*. The experiment was conducted using an F<sub>10</sub> progeny of field-collected *Ae. albopictus* from Miami, FL. On the first day of the experiment, 400 ml Tri-Pour<sup>®</sup> beakers were filled with 340 ml of deionized (DI) water and 45 first-instar (~24 hr) larvae added to each beaker. We added to each unit 0.03 ± 0.0005 g of 1:1 lactalbumin: yeast (by volume) as a resource. The beakers were placed in one of three environmental chambers, all with a temperature of 25 °C. Each chamber represented one of the following photoperiod treatments: (1) short day (10:14 Light: Dark), (2) control (12:12 L:D) and (3) long day (14:10 L:D). There were 10 replicates (beakers) for each photoperiod treatment, resulting in 30 experimental total units. The photoperiod times applied in the treatments are within 30 min of the maximum and minimum day lengths in summer and winter at 25–26° latitudes ([http://aa.usno.navy.mil/data/docs/RS\\_OneYear.php](http://aa.usno.navy.mil/data/docs/RS_OneYear.php)) and are close to or identical treatments that have been

used in other studies with *Ae. albopictus* and *Ae. aegypti* (Lounibos *et al.*, 2003; Yee *et al.*, 2012; Costanzo *et al.*, 2015). In nature, fluctuations in photoperiod are often coupled with changes in temperature; however, we aimed to isolate the effects of photoperiod as an independent cue. We selected a temperature of 25 °C because it represents an intermediate of the range of temperatures experienced in Miami, FL from the onset of autumn to late spring (20–28.3 °C), (<http://www.weather.com/weather/wxclimatology/monthly/USFL0316>).

To prevent resource depletion, 0.015 g of lactalbumin yeast was added to each cohort (beaker) on days 5 and 10 of the experiment. Each day of the experiment, any pupae from each cohort were transferred to individual vials with DI water until eclosion. Following eclosion, adult mosquitoes were sacrificed by freezing, and stored in a drying oven (60 °C) for at least 24 h. Adult mosquito wings were dissected and mounted on microscope slides, and wing length measured as a proxy for adult size (Leica application suite ver. 1.7.0).

### Experiment II: *Ae. aegypti*

This experiment tested the effects of varying photoperiod regimes on *Ae. aegypti* male and female development time and body size, as well as population growth and survival to adulthood. The experiment was conducted using F<sub>4</sub> progeny of field-collected *Ae. aegypti* from Miami, FL. Identical photoperiod treatments, temperature, water volume, resource levels and resource additions were applied as the first experiment with *Ae. albopictus*. The only difference between experiments was that in experiment II, 40 first instar larvae were added on the first day of the experiment and six replicates represented each photoperiod treatment. All other protocols implemented (including daily data collection and mosquito processing) were identical to those used in the first experiment with *Ae. albopictus*.

### Data and analyses

In both experiments, we measured mean development time (days from hatching to adult ecdysis) and adult size (wing length in mm) for males and females. For both species, we calculated survivorship to adulthood (number of adults/initial number of larvae), and the finite rate of increase ( $\lambda'$ ) of each replicate. This composite index of mosquito performance is based on  $r'$ , which estimates the realized per capita rate of population changes for each replicate [ $\lambda' = \exp(r')$ ], (Livdahl and Sugihara,

**Table 1.** MANOVA results on life history traits in *Aedes albopictus* and *Ae. aegypti*, respectively, across photoperiod treatment, sex and their interaction

Effect	F	df	Pillai's Trace	Standardized canonical coefficients	
				Development time	Size
<i>Aedes albopictus</i>					
Photoperiod	9.55	4, 108	< 0.0001	1.44	0.46
Sex	592.68	2, 53	< 0.0001	0.19	4.54
Photoperiod × Sex	0.52	4, 108	0.7209	1.13	−3.19
<i>Aedes aegypti</i>					
Photoperiod	4.24	4, 60	0.0043	1.59	1.69
Sex	173.44	2, 29	< 0.0001	1.05	2.69
Photoperiod × Sex	0.93	4, 60	0.4545	1.63	1.37

1984). We calculated  $\lambda'$  for each cohort as follows:

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

where  $N_0$  is the initial number of females in a cohort (assumed to be 50% of the initial cohort),  $A_x$  is the number of females eclosing on day  $x$ ,  $w_x$  is a measure of mean female size on day  $x$  per replicate,  $f(w_x)$  is a function relating fecundity to female size, and  $D$  is the time (in days) for a newly eclosed female to mate, obtain a blood meal and oviposit. For *Ae. albopictus*,  $D$  is 14 days (Livdahl and Willey, 1991), whilst for *Ae. aegypti*,  $D$  is 12 days (Grill and Juliano, 1996). The size–fecundity relationship for *Ae. albopictus* applied is  $f(w_x) = 78.02(w_x) - 121.24$ , ( $r^2 = 0.713$ ,  $N = 91$ ,  $P < 0.001$ ), ( $w_x$  = wing length in mm), (Lounibos *et al.*, 2002). In experiment II, emerged *Ae. aegypti* females were small in size, so we used the cube of the wing length for all calculations ( $w_x^3$  = (wing length in mm)<sup>3</sup>). The size–fecundity relationship for *Ae. aegypti* applied is  $f(w_x^3) = 2.5(w_x^3) - 8.616$  ( $r^2 = 0.875$ ,  $N = 206$ ,  $P < 0.001$ ) (Briegel, 1990).

We ran identical analyses for both experiments unless otherwise specified. All of the analyses described below were done for both *Ae. albopictus* and *Ae. aegypti* separately. For *Ae. albopictus*, the  $\lambda'$  data did not meet the assumption of normality (which transformations did not eliminate), so we performed a Kruskal–Wallis test (PROC NPAR1WAY, SAS 9.1) to detect any differences in *Ae. albopictus*  $\lambda'$  across photoperiod treatments. For *Ae. aegypti*, the  $\lambda'$  data met all assumptions, and we ran an analysis of variance (ANOVA), (PROC GLM, SAS 9.1) with photoperiod treatment as a fixed effect. A general linear mixed-model (PROC GLIMMIX, SAS 9.1) was used to detect differences amongst proportion survival to adulthood for cohorts across photoperiod treatments with the replicate as a random effect.

A multivariate analysis of variance (MANOVA) (PROC GLM, SAS 9.1) was run on the life history traits (development time and adult size) with photoperiod, sex and the interaction of photoperiod by sex as independent variables to detect any effect of photoperiod treatment, sex, and if the response to photoperiod treatments varied by sex. Standardized canonical coefficients were used to assess the relative contribution of each dependent variable to the effect (Scheiner, 2001). The sexual dimorphism of size and development time within a treatment were calculated by subtracting the male mean wing length and development time from that of the female (e.g. female wing length–male wing length), (Yee *et al.*, 2012). The difference in sexual dimorphism across treatments was analysed by a MANOVA with photoperiod as a fixed effect. Follow-up Tukey tests ( $\alpha = 0.05$ ) were performed to detect any pairwise differences between the dependent variables across treatments and sex, depending on the analysis.

## Results

### Experiment I: *Ae. albopictus*

For *Ae. albopictus*, there was no significant effect of photoperiod treatment on the proportion of the population that survived to adulthood (Mixed model GLM:  $F = 1.73$ ;  $df = 2, 18$ ;  $P = 0.21$ ), (mean % survival  $\pm 1$  standard error, short day: 52.52%  $\pm 0.07$ , control: 52.88%  $\pm 0.03$ , long day: 54.67%  $\pm 0.05$ ). There was also no effect of photoperiod on the population growth index  $\lambda'$  ( $\chi^2 = 2.63$ ;  $df = 2$ ;  $P = 0.27$ ), with  $\lambda'$  estimates above 1 in all treatments, indicating a positive population growth (median  $\pm$  interquartile ranges: short day: 1.112  $\pm 0.091$ , control: 1.123  $\pm 0.023$ , long day: 1.111  $\pm 0.026$ ).

Both photoperiod and sex had a significant effect on *Ae. albopictus* life history dependent variables, whilst the interaction of treatment by sex was not significant (Table 1). Standardized canonical coefficients show that variation in development time was more affected by photoperiod treatment, whilst

the sex effect could explain more of the variation in size (Table 1). In the short-day treatments, adult females were significantly larger in size compared to the controls, whereas there was no difference in male adult size across treatments (Fig. 1a). Females took longer to develop in the long-day treatments compared to controls, whilst no difference in male development times was detected across treatments (Fig. 1a).

The overall trends in sexual dimorphism across all treatments were as expected, with females taking significantly longer to develop and were larger in size as adults than males (Table 1), (mean development time  $\pm$  1 standard error: males: 13.54  $\pm$  0.23, females: 15.79  $\pm$  0.23; mean wing length  $\pm$  1 standard error: males: 1.86  $\pm$  0.01, females: 2.50  $\pm$  0.01). Across photoperiod treatments, the magnitude of sexual dimorphism did not vary (e.g. female size–male size) ( $F = 0.6$ ;  $df = 4, 54$ ; Pillai's Trace  $P = 0.67$ ) (Fig. 2a).

#### Experiment II: *Aedes aegypti*

For *Ae. aegypti*, there was no significant effect of photoperiod treatment on survival (Mixed model GLM:  $F = 0.02$ ;  $df = 2,10$ ;  $P = 0.98$ ), (mean % survival  $\pm$  1 standard error, short day: 65.41%  $\pm$  0.03, control: 66.25%  $\pm$  0.07, long day: 65.83%  $\pm$  0.02). There was no effect of photoperiod on the population growth index  $\lambda'$  ( $F = 0.42$ ;  $df = 2,15$ ;  $P = 0.66$ ), and all cohorts illustrated positive population growth with  $\lambda'$  estimates above 1 (mean  $\pm$  1 standard error: short day: 1.075  $\pm$  0.007, control: 1.071  $\pm$  0.007, long day: 1.066  $\pm$  0.007).

The MANOVA indicated that photoperiod and sex had a significant effect on *Ae. aegypti* life history traits, with no effect of the interaction. Adult size contributed to slightly or substantially more of the variation detected in the treatment and sex effect, respectively (Table 1). However, the post-hoc tests indicated no significant differences in *Ae. aegypti* size or development times across treatments for both males and females (Fig. 1b). Between the two sexes, females took significantly longer to develop and were significantly larger as emerging adults, compared to males (mean development time  $\pm$  1 standard error: males: 16.21  $\pm$  0.42, females: 19.88  $\pm$  0.43; mean wing length  $\pm$  1 standard error: males: 1.7  $\pm$  0.02, females: 2.12  $\pm$  0.02). There was no difference found in the degree of sexual dimorphism detected across photoperiod treatments ( $F = 1.07$ ;  $df = 4, 30$ ; Pillai's Trace  $P = 0.39$ ), (Fig. 2b).

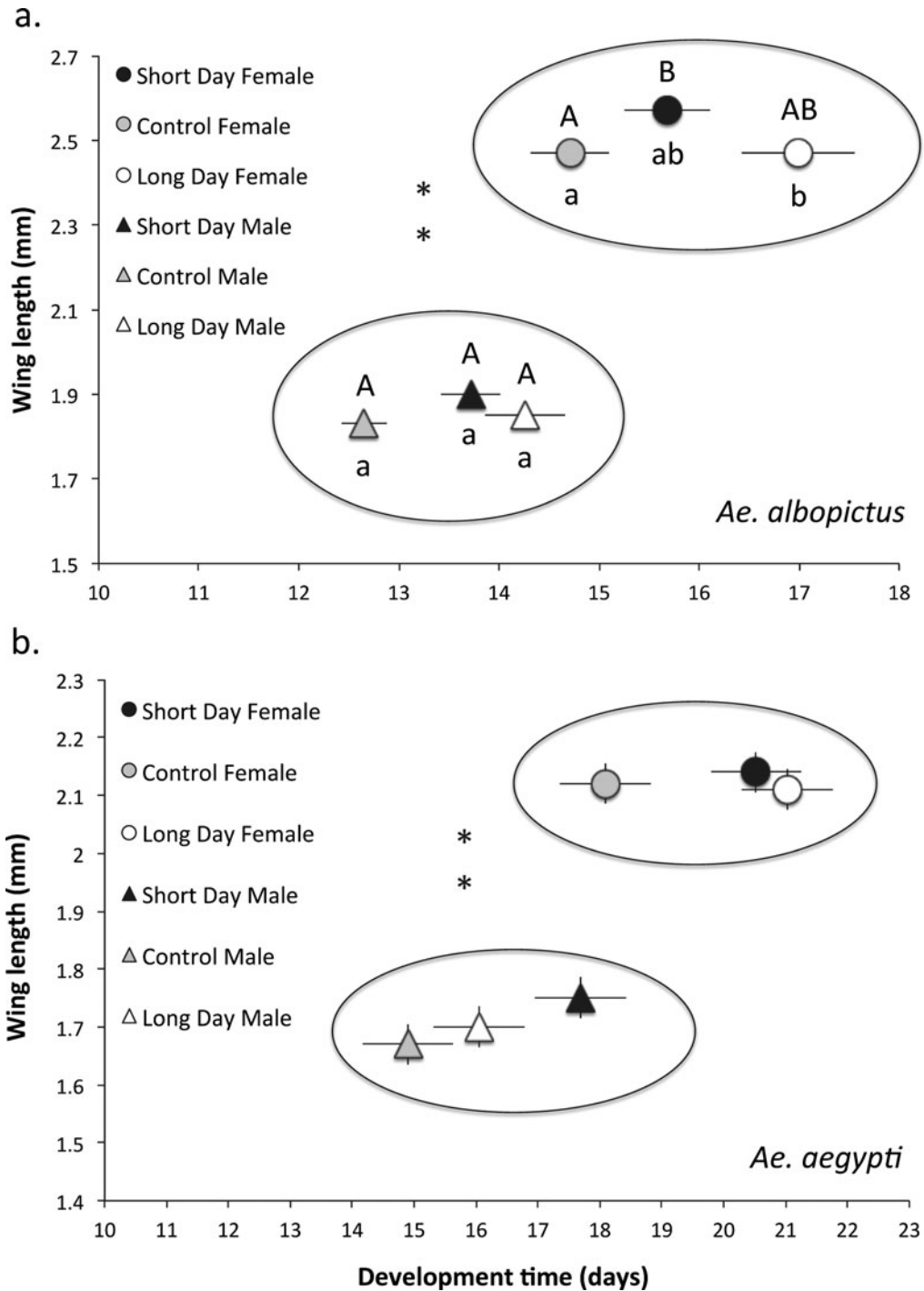
### Discussion

Although photoperiod may induce changes in life history traits and behaviour of *Ae. albopictus* and *Ae. aegypti* (Yee *et al.*, 2012; Costanzo *et al.*, 2015),

we found no evidence for effects of photoperiod on the population performance of both species. In our study, photoperiod affected neither the population growth index  $\lambda'$  nor survivorship to adulthood. The latter suggests that any life history changes detected were not a result of density dependent effects. This study did, however, find evidence for differences in the male and female responses to photoperiod treatments (sexually dimorphic responses) in *Ae. albopictus*, but not *Ae. aegypti*.

Overall, for *Ae. albopictus*, we found the females were more sensitive to different photoperiod treatments, consistent with Yee *et al.* (2012). Females took longer to develop in long-day treatments, with no differences in male development times detected across treatments. Since generally, shorter development times in males maximizes their fitness (Steinwascher, 1982), stronger selection towards a canalized response would be expected in males but not in females, and is consistent with our findings. In other mosquitoes, greater constraints on the development time of males have been observed in their response to environmental conditions (Bedhomme *et al.*, 2003).

Considering the greater fitness consequences of body size in females compared to males, one may expect the body size of males to be more sensitive to environmental fluctuations than females. However, in our study, we found that female size varied across photoperiod treatments, whilst males exhibited no differences in size. Short-day treatments produced larger *Ae. albopictus* adult females, consistent with Costanzo *et al.* (2015), who used identical photoperiod treatments and experimental protocols. The sexual dimorphism in the responses of adult size to photoperiod can be explained by the functional roles of the sexes in reproduction. *Aedes albopictus* females can produce overwintering diapausing eggs, which is reflected by their distribution extending through temperate regions around the world (Hawley *et al.*, 1987; Mitchell, 1995; Leisham *et al.*, 2011). In *Ae. albopictus*, diapause is induced primarily by photoperiod (Mori *et al.*, 1981; Pumpuni *et al.*, 1992) and functions to sustain a population through unfavourable conditions, such as extreme cold temperatures or desiccation (Urbanski *et al.*, 2010; Thomas *et al.*, 2012). Diapausing eggs have higher energetic demands than non-diapausing eggs, requiring greater energy inputs from mosquitoes (Hahn and Denlinger, 2007). Thus, the shift towards a larger body size in female *Ae. albopictus* in shorter day lengths may be a mechanism adopted to accumulate the energy reserves to invest in diapausing eggs as unfavourable conditions approach. The lack of differences found in *Ae. albopictus* male adult size across treatments in our study further supports this postulate.



**Fig. 1.** Wing length and development time of males and females for *Aedes albopictus* (a) and *Ae. aegypti* (b), across photoperiod treatments. For both species, significant differences between the two sexes for both traits are indicated with an asterisk. For *Ae. albopictus*, significant pairwise differences in wing length across treatments are indicated with different upper case letters, whilst significant pairwise differences in development time across treatments are indicated with different lowercase letters. For *Ae. aegypti*, there were no significant pairwise differences detected in development times or sizes across treatments.

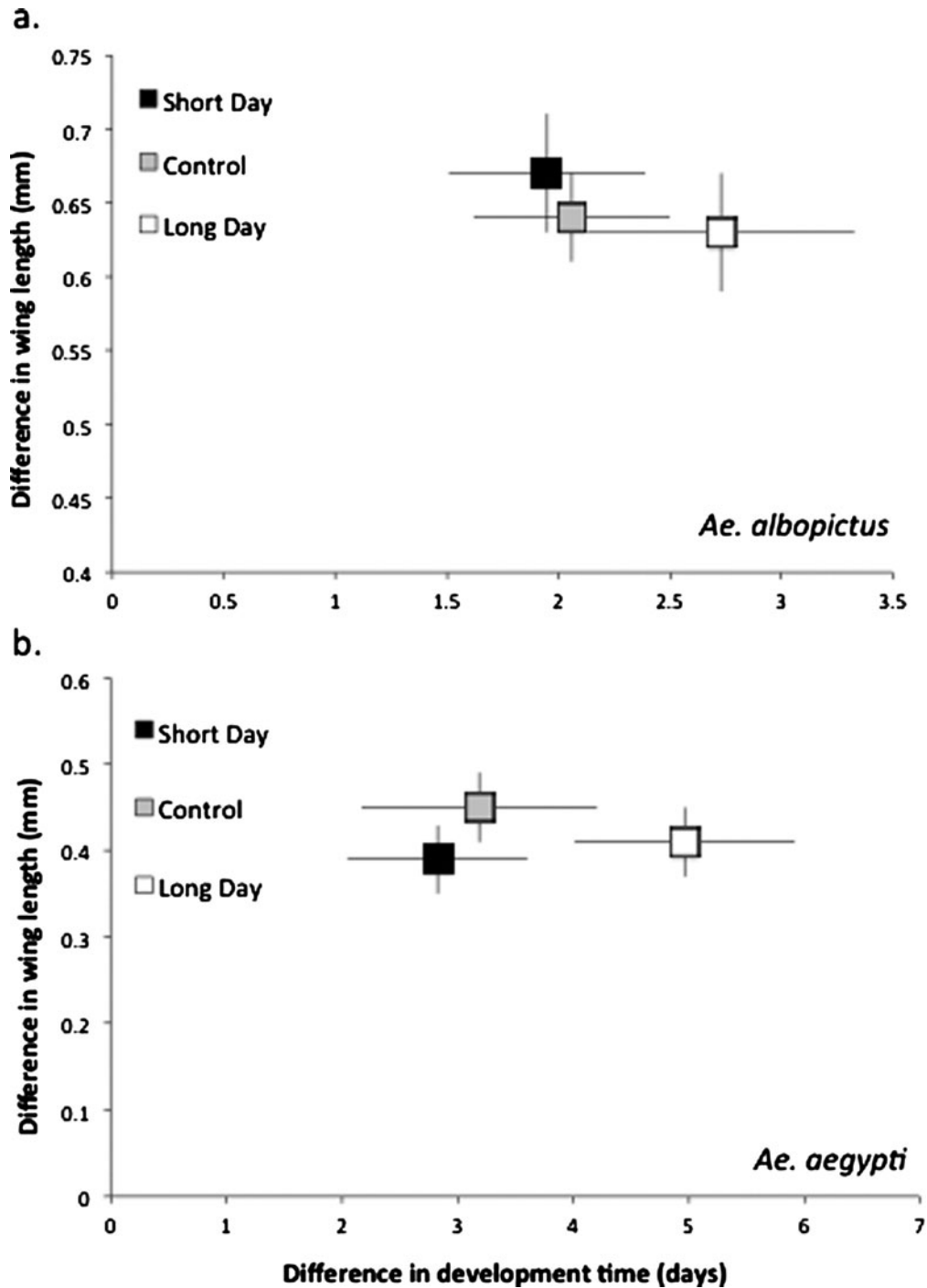


Fig. 2. Sexual dimorphism in development time (female development time–male development time) and size (female wing length–male wing length) for *Aedes albopictus* (a) and *Aedes aegypti* (b) across photoperiod treatments.

Despite these differences in male and female responses across treatments, we found no evidence for differences in the magnitude or direction of sexual dimorphism across treatments. Although not significant, males also trended towards a longer development time in long-day treatments and a

larger size in short day treatments in long- and short-day treatments, which contributed to the lack of difference detected statistically. In another photoperiod study, a greater difference between *Ae. albopictus* male and female mass and development time (greater sexual dimorphism) was found in

long-day conditions (Yee *et al.*, 2012). Interestingly, the trends in body size of this study with largest females emerging from long-day conditions were the opposite of our study. These differences across studies illustrate how the interaction of photoperiod with different variables (such as temperature and resources) may alter the phenotypic consequences. Additionally, our study failed to illustrate the common trade-off associated between development time and size found in mosquitoes, with faster developmental rates associated with smaller sized adults (Kleckner *et al.*, 1995; Yee *et al.*, 2012; Wormington and Juliano, 2014). It is possible that other physiological and developmental costs not measured in this study may be associated with shorter development times.

In contrast to *Ae. albopictus*, female *Ae. aegypti* life history traits were less sensitive to photoperiod than males. For *Ae. aegypti*, although photoperiod affected life history traits in general (Table 1), we failed to detect any pairwise differences in the development time and size in both males and females across photoperiod treatments (Fig. 1b). Since photoperiod did not result in any significant changes across both sexes in *Ae. aegypti*, we also found no difference in the magnitude or direction of sexual dimorphism across photoperiod treatments (Fig. 2b). Unlike *Ae. albopictus*, *Ae. aegypti* cannot produce diapausing eggs, which is perhaps why there are consistently no effects of photoperiod found on female body size in *Ae. aegypti* as there are in *Ae. albopictus* (Costanzo *et al.*, 2015). Rather than diapause, *Ae. aegypti* has developed other mechanisms that may sustain their populations through harsh conditions, such as the production of non-diapausing eggs with an increased tolerance to desiccation (Juliano *et al.*, 2002; Costanzo *et al.*, 2005), and a greater adult tolerance to desiccation and colder temperatures compared to *Ae. albopictus* (Mogi *et al.*, 1996; Brady *et al.*, 2013). Furthermore, Costanzo *et al.*, (2015) found in a photoperiod laboratory study that in shorter day environments, *Ae. aegypti* females are more likely to blood feed and live longer as adults. These may be additional strategies adopted by *Ae. aegypti* to increase energy reserves that can carry the population as adults through periods with reduced temperature and precipitation across their range (Costanzo *et al.*, 2015).

In competitive larval environments, *Ae. aegypti* has been shown to exhibit sexually dimorphic responses in traits least associated with fitness cost (size for males, development time for females) (Bedhomme *et al.*, 2003). When reared under adverse conditions (such as limiting resources and overcrowding), this sexual dimorphic response is likely due to optimization of trade-offs in a stressful environment. In our study, the environmental gradient

(day length) acts as a cue signalling environmental change rather than posing a stress on the mosquitoes with associated costs. The lack of difference in the two life history traits measured in this study in *Ae. aegypti* across photoperiod treatments may not encompass the changes the two sexes go through in preparation for winter months. It would be of interest to determine if *Ae. aegypti* males also have an increased life span in shorter day lengths as females have (Costanzo *et al.*, 2015), as male longevity has been shown to be more sensitive to environmental stress than that of females in *Ae. aegypti* (Bedhomme *et al.*, 2003).

Although we did not find any effects of photoperiod on population dynamics of both species, the interspecific differences in photoperiod effects on life history may have both ecological and medical implications on a seasonal, temporal scale. In the US, larval *Ae. albopictus* is illustrated as the superior resource competitor to several native and resident species, particularly *Ae. aegypti* (Juliano and Lounibos, 2005). However, environmental conditions (including resource type, resource ratios, precipitation, predation and pesticides) can alleviate the effects of competition from *Ae. albopictus* on other species, or even reverse the competitive advantage (Griswold and Lounibos, 2005; Costanzo *et al.*, 2005, 2011b; Yee *et al.*, 2007; Murrell and Juliano 2008; Alto *et al.*, 2013). It would be of interest to evaluate the effects of photoperiod on interspecific interactions of the invasive *Ae. albopictus* with resident species. Additionally, life history traits such as body size can have an impact on other parameters of vectorial capacity, including blood feeding behaviour and vector competence (Alto *et al.*, 2008b; Westbrook *et al.*, 2010; Farjana and Tuno, 2013). The effects of photoperiod on lifespan and fecundity have already been investigated (Costanzo *et al.*, 2015), but the impact of photoperiod on other parameters of vectorial capacity and vector competence should be evaluated as environmental factors can alter these traits (Alto *et al.*, 2008a; Muturi *et al.*, 2012; Alto and Lounibos, 2013; Brady *et al.*, 2013).

## Conclusion

We found no evidence of photoperiod affecting the population performance of *Ae. albopictus* and *Ae. aegypti*. In *Ae. albopictus*, photoperiod treatments produced a response in female size and development time, with no response detected in males across treatments. This sexually dimorphic response to various photoperiods can be explained both by different fitness consequences to changes in these traits between the two sexes, and by females transitioning into diapause. For *Ae. aegypti*, neither male nor female development time or size varied across treatments. We found no evidence for sexual



dimorphic responses across photoperiod treatments in *Ae. Aegypti* that they exhibit under stressful conditions. The differences across species reflect different strategies adopted to sustain the population through unfavourable conditions, and could have potential ecological and medical consequences associated with the spread of these species.

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