ORIGINAL ARTICLE

Spatial and temporal variations on the coexistence of *Aedes* and *Culex* larvae in Southern Thailand

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Abstract This study investigated spatial and temporal variations on the coexistence of *Aedes aegypti*, *Aedes albopictus*, and *Culex* larvae in five subdistricts in Nakhon Si Thammarat, Thailand. We tested two main hypotheses on the spatial and temporal coexistence of mosquito larvae: (1) condition-specific competition and (2) spatial variation among the five subdistricts. We compared the number of positive houses, positive containers, mosquito coexistence during both the wet and dry seasons. The results showed that from a total of 1,072 positive containers collected in both seasons, *Ae. albopictus* larvae were found in the highest number of containers (745 containers), followed by containers with *Ae. aegypti* larvae (283 containers) and containers with *Culex* larvae (254 containers). During the wet season, there were higher numbers of positive houses, positive containers, and containers with only *Ae. albopictus* larvae than during the dry season. On the other hand, during the dry season when the water containers were very scarce, there were higher numbers of containers with *Culex* larvae, and containers held more than one type of mosquito larvae. This indicates that both temporal and spatial variations may contribute to the local coexistence of *Aedes* and *Culex* mosquito larvae species in Lansaka District areas in Thailand.

Keywords: Nakhon Si Thammarat, positive containers, positive house, wet and dry season

Introduction

Competitive interactions between two mosquito species are often asymmetrical and may have important consequences on mosquito-borne infections and control strategies (Juliano 2009). One species can be inferior to another species but at the same time superior to others. The competitive asymmetry has been attributed to efficiency in converting food to biomass, larval food substrates (Barrera 1996; Daugherty et al 2000; Braks et al 2004), larval density (Juliano et al 2004; Serpa et al 2008), and temperature (Carrieri et al 2003). For example, *Ae. aegypti* proves to be the inferior competitor to *Ae. albopictus* but superior to *Cx. quinquefasciatus* (Santana-Martínez et al 2017) and *Cx. pipiens* (Francia and Maciá 2017). *Ae. albopictus* is a competitively superior species against other mosquito species, such as *Ae. aegypti* (Barrera 1996; Daugherty et al 2000; Murrell and Juliano 2008; Serpa et al 2008), *Ae. japonicus* (Armistead et al 2008), *Ae. triseriatus* (Ho et al 1989; Novak et al 1993), *Cx. coronator* (Yee and Skiff, 2014), and *Cx. pipiens* (Carrieri et al 2003, 2011; Costanzo et al 2005; Muturi et al 2011).

Asymmetrical competition only occurs when the potential competitors encounter one another in nature. With high competitive asymmetry, the competitively inferior species is expected to shift their temporal patterns to lower interspecific competition. For example, *Cx. pipiens* is the inferior species to *Ae. albopictus*, and it displays a time shift to reduce the overlapping period in the US (Costanzo et al 2005) and Italy (Carrieri et al 2003; Marini et al 2017). In Thailand, *Ae. aegypti* is the inferior species to *Ae. albopictus*, and it also displays a time shift resulting in the greatest prevalence during the dry season instead of the wet season when *Ae. albopictus* is most prevalent (Preechaporn et al 2006, 2007; Chumsri et al 2018).

Aedes and *Culex* larvae are the most widespread mosquito larvae in Thailand (Scanlon and Esah 1965; Chansang et al 1999; Chareonviriyaphap et al 2003; Luemoh et al 2003; Thavara et al 2004; Thanispong et al 2008; Preechaporn et al 2007; Wongkoon et al 2007; Chumsri et al 2018; Promprao et al 2018). In Thailand, *Ae. aegypti*, *Ae. albopictus*, and *Culex* spp. encounter one another in their shared water containers with overlapping distribution, but they prefer different breeding sites (Preechaporn et al 2007; Wongkoon et al 2007; Chumsri et al 2018; Promprao et al 2018). Their breeding site preferences could be shaped by both

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interspecific competition and spatial and temporal niche differentiation. *Ae. aegypti* prefers clean indoor water containers, whereas *Ae. albopictus* prefers outdoor artificial water containers containing a greater amount of organic debris (Chareonviriyaphap et al 2003; Preechaporn et al 2007; Wongkoon et al 2007; Chumsri et al 2018), while *Culex* larvae inhabit outdoor containers with high levels of organic matter and highly contaminated bodies of water, such as drainage sewers from houses (Preechaporn et al 2007).

Our study, investigating the coexistence of *Ae. aegypti*, *Ae. albopictus*, and *Culex* larvae in five subdistricts (Khaokaew, Lansaka, Thadi, Kamlon, and Khunthale) in Nakhon Si Thammarat, southern Thailand during the wet and dry seasons, was based on two main hypotheses: (1) Condition-specific competition predicts that (1a) all species would occupy a greater proportion of containers and be more abundant during the wet season than during the dry season; (1b) the abundance of *Ae. albopictus* larvae would be higher during the wet season (October-December), and the abundance of *Ae. aegypti* and *Culex* larvae would decrease; and (1c) *Ae. albopictus* larvae would be more competitive compared to *Ae. aegypti* and *Culex* larvae, and thus, *Ae. albopictus* larvae would be present in more containers. (2) The spatial hypothesis predicts that (2a) co-occurrence of larval species would be found in different subdistricts; and (2b) *Ae. albopictus* larvae would be more competitive compared to *Ae. aegypti* and *Culex* larvae in most of the subdistricts.

To the best of our knowledge, this is one of the first efforts to assess the coexistence and interactions of *Ae. aegypti*, *Ae. albopictus*, and *Culex* larvae.

Materials and Methods

Study site

This study was conducted in five subdistricts (Lansaka, Khaokaew, Thadi, Kamlon, and Khunthale) in Lansaka District, Nakhon Si Thammarat Province, in the southern part of Thailand (8.40700°N and 99.76891°E) (Figure 1a-c). The dry season in Nakhon Si Thammarat is from February to May. The wet season starts in June and ends in January. Over 10 years, (2009-2018), the annual mean temperature was about 27.44 °C. The average maximum and minimum temperatures were 35.02 °C and 21.99 °C, respectively. The mean monthly rainfall during the wet season was 340.44 mm. During the dry and wet seasons, mean temperatures were approximately 27.94 °C and 26.95 °C, respectively (collected by the Centre of Excellence for Ecoinformatics, Walailak University).

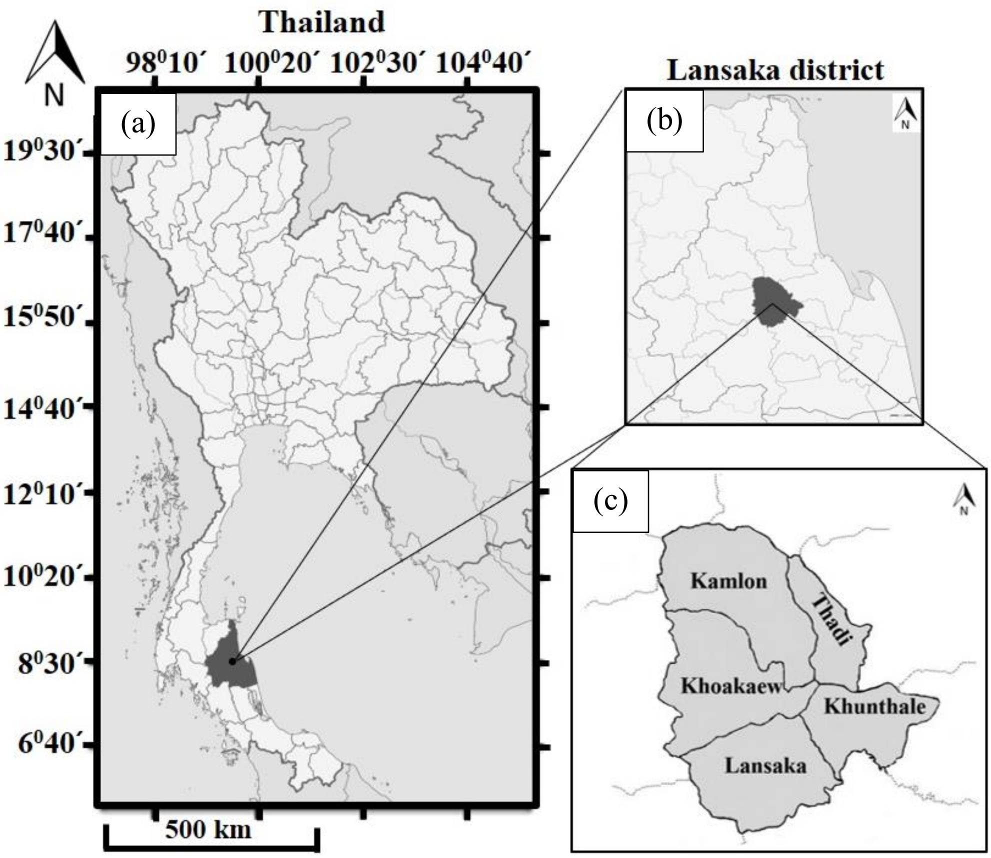

Figure 1 (a) Map of Thailand and black dot represents location of Lansaka District, Nakhon Si Thammarat Province, Southern Thailand, (b) Lansaka District, and (c) the study areas of five subdistricts)Lansaka, Khaokaew, Thadi, Kamlon, and Khunthale).

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Mosquito larvae collection

In each subdistrict, 120 houses were randomly selected to study breeding sites of *Aedes* and *Culex* mosquitoes during the dry (March-April, 2018) and wet (October-December, 2018) seasons. There were a total of 300 households sampled during the dry season. The same 300 households were resampled during the wet season to compare the differences in the number of *Ae. aegypti*, *Ae. albopictus* and *Cule*x larvae in water containers between seasons and among subdistricts.

In each house, mosquito larvae were collected based on the GLOBE Mosquito Protocol (www.globe.gov, 2018) from different kinds of water containers (e.g., water-storing containers – water jars, water tanks, water buckets, etc.; plant pots; feeding pans of animals; lids of water containers; trash containers; coconut shells; etc.) by using 0.55 mm mesh-size fishnets. Mosquito larvae were collected from both indoor and outdoor containers. All live mosquito larvae were placed in plastic bags taken to Walailak University and preserved in 70% ethanol. Mosquito larvae for *Ae. aegypti* and *Ae. albopictus* were identified up to its species level based on Rattanarithikul and Panthusiri's keys (Rattanarithikul and Panthusiri 1994).

In this study, only *Ae. aegypti*, *Ae. albopictus*, and *Culex* mosquito larvae were considered. *Mansonia* spp., *Armigeres* spp., and *Toxorhynchites* spp. larvae were also collected from the field study but constituted less than 1% of the total number of larvae and were not used. We evaluated the relative abundance of mosquito larvae across 600 households in five subdistricts. We were specifically interested in examining how relative abundance and multiple mosquito species occurrence (co-occurrence at a site) varied with seasons and subdistricts.

Data analysis

Chi-squared tests were used to investigate the differences in numbers of positive houses, positive containers, containers holding mosquito larvae, containers, and mosquito larvae between the wet and dry seasons and among five subdistricts. Containers with mosquito larvae were classified into eight categories based on types of mosquitoes present in the containers: containers contained (1) *Ae. aegypti* larvae (AE containers), (2) *Ae. albopictus* larvae (AL containers), (3) *Culex larvae* (CX containers), (4) *Ae. aegypti* and *Ae. albopictus* larvae (AE+AL containers), (5) *Ae. aegypti* and *Culex* larvae (AE+CX containers), (6) *Ae. albopictus* and *Culex* larvae (AL+CX containers), (7) *Ae. aegypti*, *Ae. albopictus* and *Culex* larvae (AE+AL+CX containers), and (8) no mosquito larvae (negative containers). We used SPSS 22 as the statistical analysis software, and all significant tests were two-tailed. We considered a statistically significant level to be at *P*<0.05.

Results

Season, positive houses and positive containers

During the wet season, there were higher numbers of positive houses, positive containers, AL containers, and negative containers than during the dry season (Chi-squared test: positive houses: $x_1^2 = 22.294$, *P*<0.001; positive containers: $x_1^2 = 10.481$, *P*<0.005; AL containers: $x_1^2 = 135.905$, *P*<0.001; negative containers: $x_1^2 = 657.627$, *P*<0.001, Table 1). During the dry season, there were higher numbers of CX containers, AE+CX containers, AL+CX containers, and AE+AL+CX containers (Chi-squared test: CX containers: $x_1^2 = 43.758$, *P*<0.001; AE+CX containers: $x_1^2 = 21.552$, *P*<0.001; AL+CX containers: $x_1^2 = 17.053$, *P*<0.001; AE+AL+CX containers: $x_1^2 = 14.222$, *P*<0.001, Table 1). Seasons had no effects on numbers of AE containers and AE+AL containers (Chi-squared test: AE containers: $x_1^2 = 0.602$, *ns*; AE+AL containers: $x_1^2 = 1.704$, *ns*, Table 1).

Subdistricts, positive houses, and positive containers

Among subdistricts, there were some differences in numbers of positive containers, AE containers, AL containers, AE+AL containers, and negative containers (Chi-squared test: positive containers: $x_4^2 = 79.707$, *P*<0.001; AE containers: $x_4^2 = 15.807$, *P*<0.005; AL containers: $x_4^2 = 47.546$, *P*<0.001; AE+AL containers: $x_4^2 = 20.197$, *P*<0.001; negative containers: $x_4^2 = 160.836$, *P*<0.001, Table 1). There was no difference among subdistricts in numbers of positive houses, CX containers, AE+CX containers, AL+CX containers, and AE+AL+CX containers (Chi-squared test: positive houses: $x_4^2 = 8.298$, *ns*; CX containers: $x_4^2 = 6.485$, *ns*; AE+CX containers: $x_4^2 = 5.310$, *ns*; AL+CX containers: $x_4^2 = 6.368$, *ns*; AE+AL+CX containers: $x_4^2 = 4.222$, *ns*, Table 1).

Seasons and numbers of mosquito larvae

From a total of 1,072 positive containers collected in both seasons, *Ae. albopictus* larvae were found in the highest number of containers (745 AL containers), followed by containers with *Ae. aegypti* larvae (283 AE containers) and containers with *Culex* larvae (254 CX containers) (Chi-squared test: $x_2^2 = 355.200$, *P*<0.001). From a total of 15,783 mosquito larvae collected in both seasons, *Ae. albopictus* larvae were found in the highest number (10,269 larvae), followed by *Culex* larvae (2,996 larvae) and *Ae. aegypti* larvae (2,518 larvae) (Chi-squared test: $x_2^2 = 7172.465$, *P*<0.001).

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Table 1 Seasons and subdistricts with positive (+) houses and positive (+) containers occupied by *Ae. aegypti* (AE), *Ae. albopictus* (AL), and *Culex* (CX) larvae during the wet and dry seasons five subdistricts, Nakhon Si Thammarat, Thailand.

Parameters	Khaokaew			Lansaka			Thadi			Kamlon			Khunthale			Total	
	Dry	Wet	Total	Dry	Wet	Total	Dry	Wet	Total	Dry	Wet	Total	Dry	Wet	Total	Dry	Wet
+House	22	31	53	21	31	52	29	51	80	19	41	60	22	42	64	113	196
+Container	131	93	224	73	68	141	132	186	318	75	113	188	72	129	201	483	589
AE	26	15	41	14	7	21	21	28	49	15	12	27	12	16	28	88	78
AL	40	58	98	21	55	76	40	136	176	26	90	116	23	92	115	150	431
CX	28	8	36	17	3	20	26	4	30	17	5	22	16	8	24	104	28
AE+AL	13	5	18	6	1	7	12	15	27	4	3	7	6	6	12	41	30
AE+CX	6	1	7	5	0	5	10	0	10	3	0	3	3	1	4	27	2
AL+CX	13	6	19	7	2	9	18	3	21	9	3	12	9	6	15	56	20
AE+AL+CX	5	0	5	3	0	3	5	1	6	1	0	1	3	0	3	17	1
None	98	263	361	103	332	435	121	556	677	114	345	459	87	248	335	523	1744

During the dry season, a total of 483 positive containers were found with a total of 6,165 mosquito larvae found in those containers, while during the wet season, a total of 589 positive containers were found with 9,618 mosquito larvae. During the dry season, there were higher numbers of CX, AE+AL, AE+CX, AL+CX, and AE+AL+CX larvae but lower numbers of AE and AL larvae than during the wet season (Table 2).

Discussion

There has been extensive research conducted on the coexistence of mosquito species in the same breeding sites in the US, Columbia, and Italy. Examples of such coexistence include *Ae. albopictus* and *Cx. quinquefasciatus* (Daniels et al 2015), *Ae. albopictus* and *Ae. triseriatus* (Novak et al 1993), *Ae. albopictus* and *Cx. pipiens* (Hawley 1988; Vinogradova 2000; Carrieri et al 2003, 2011; Costanzo et al 2005; Marini et al 2017), and *Ae. aegypti* and *Cx. quinquefasciatus* (Santana-Martínez et al 2017). Our results were the first to report the coexistence of *Ae. aegypti*, *Ae. albopictus* and *Culex* larvae in the same breeding sites in Thailand. We showed that not only *Ae. aegypti* and *Ae. albopictus* larvae coexisted in the same containers but also coexisted with *Culex* larvae in those same containers. Coexistence of *Aedes* and *Culex* larvae has been found in the same breeding containers, such as flower pots, animal pans, drums, used tires, buckets, flower saucers, tarpaulins, manholes, and bathtubs (Carrieri et al 2003; Leisnham et al 2014).

Table 2 Numbers of mosquito larvae during the wet and dry seasons in five subdistricts, Nakhon Si Thammarat, Thailand.

Mosquito Coexistence	Numbers of mosquito larvae		
	Dry season	Wet season	Chi-squared test
AE	1,204	1,314	$x_1^2 = 4.805$*
AL	2,419	7,850	$x_1^2 = 2872.311$**
CX	2,542	454	$x_1^2 = 1455.188$**
AE+AL	1,102	676	$x_1^2 = 102.067$**
AE+CX	744	178	$x_1^2 = 347.458$**
AL+CX	1,875	751	$x_1^2 = 481.103$**
AE+AL+CX	715	1	$x_1^2 = 712.006$**

*$P < 0.05$, **$P < 0.001$ *Ae. aegypti* (AE), *Ae. albopictus* (AL), and *Culex* (CX) larvae.

The results of this study showed a clear pattern in the seasonal coexistence of *Ae. albopictus*, *Ae. aegypti*, and *Culex* larvae that were consistent with the seasonal condition-specific competition as the mechanism contributing to species coexistence. The persistence of *Ae. albopictus* larvae in the presence of the competitively superior *Ae. aegypti* and *Culex* larvae may be explained by the seasonal condition-specific competition, if there are seasonally-related differences in survival among the species. Our results showed that during the wet season when mosquito breeding sites were highly abundant, the majority of mosquito breeding sites were occupied with only *Ae. albopictus* larvae indicating the superior competitor to other mosquito species. On the other hand, during the dry season, mosquito breeding sites became

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very scarce forcing *Ae. aegypti* and *Culex* females to have no other choice but to lay eggs in containers where *Ae. albopictus* larvae already occupied. Our results showed that there were higher numbers of mosquito breeding sites occupied with more than one mosquito species during the dry season than during the wet season. Leisnham and Juliano (2009) found that *Ae. albopictus* was usually superior in competition to *Ae. aegypti*, and these species coexist at some sites in the southeastern part of the United States, including metropolitan areas. *Ae. albopictus* larvae would show a greater increase in the proportion of sites occupied and abundance per site during the wet season than *Culex* and *Ae. aegypti* larvae due to their high dry season egg mortality and strong wet season competitive superiority.

Our results showed that the number of *Ae. aegypti* and *Ae. albopictus* larvae were higher than *Culex* larvae during the wet season. Similar findings were reported by Lin et al (2018) in Taiwan. This could be due to two possible reasons. First, *Ae. aegypti* larvae were found mostly in indoor containers, but *Culex* larvae were mostly found in outdoor containers. Usually, outdoor containers are affected by rainwater during the wet season as rainfall flushes out the mosquito larvae from the outdoor containers. Second, during the wet season, normally the water inside outdoor containers stays clean due to frequent rainfall. Typically, *Cule*x mosquitoes do not prefer to lay eggs in clean water, whereas *Ae. albopictus* larvae are generally found in outdoor containers with clean water (Chumsri et al 2018).

The number of *Ae. albopictus* larvae during the wet season was higher than during the dry season. Normally *Ae. albopictus* mosquitoes like to lay their eggs in outdoor containers. During the wet season, higher numbers of total containers were observed in all subdistricts. A previous study (Chumsri et al 2018) also observed a higher number of total containers during the wet season than during the dry season in Lansaka District. There are two possible reasons for a higher number of total containers during the wet season: (1) people in Southern Thailand prefer to use rainwater for cooking, bathing, and other purposes, and for these reasons they use a higher number of various types of containers to collect rainwater (Wongkoon et al 2007; Chumsri et al 2018) and (2) waste products, such as Styrofoam cups, bottles, used cans and used tires, might collect rainwater, creating many suitable larval development sites for *Ae. albopictus* larvae in the area.

Our results showed a higher number of *Culex* larvae during the dry season than during the wet season. Similar findings were reported in Nigeria (Mahadev et al 2004), India (Govoetchan et al 2014), and Benin (Manyi et al 2014). This could happen due to four possible reasons. First, during the dry season, there is typically a lack of fresh water, and thus, water is stored in one container for a long period without cleaning it. In contrast, rainwater during the wet season flushes out the stored water in containers more often. Therefore, during the dry season, *Culex* larvae have a higher chance to stay in the same water for a longer period and finish their larval stages compared to during the wet season. Second, *Culex* mosquitoes prefer to breed in stagnant water with high organic matter in outdoor containers (Preechaporn et al 2007). These favorable breeding sites are high in numbers during the dry season. Third, oviposition activity of *Culex* females increases if relative humidity becomes 60% or higher (Micieli and Campos 2003), and during the period of this study, the average humidity of our study sites was more than 80% (data collected by our automatic weather station deployed at the site). Fourth, higher temperatures during the dry season in southern Thailand may shorten the rates of embryonic, larval and pupal development stages of mosquitoes, which leads to a higher number of smaller-sized females that digest blood more often and produce more offspring (Githeko et al 2000; Promprou et al 2005; Kiarie-Makara et al 2015). Madder et al (1983) reported that *Cx. pipiens* and *Cx. restuans* in Ontario had three major generations per year. This indicates that a higher temperature during the dry season might increase the number of generations per year. The estimated optimal temperature for *Culex* mosquito developmental stages is 28.1°C (Loetti et al 2011; Kiarie-Makara et al 2015), and the average temperature during the dry season in Southern Thailand is 28.2°C.

Our results support the spatial hypothesis that the co-occurrence of larval species was found in all five subdistricts and *Ae. albopictus* larvae were more competitive compared to *Ae. aegypti* and *Culex* larvae in all five subdistricts. When we compared the number of positive houses, positive containers and the number of AE, AL, CX, AE+AL, AE+CX, AL+CX, and AE+AL+CX containers among five subdistricts, we found that Khaokaew and Thadi subdistricts were higher in all these parameters than other subdistricts during the wet and dry seasons. This could be due to four possible reasons. First, *Ae. aegypti* larvae are found mostly in indoor containers. During the dry season, a higher number of containers were observed in Khaokaew and Thadi subdistricts than in other subdistricts because people in these subdistricts do not have sustainable water supplies and collect water from the nearby river. This was why they used a higher number of water-storing containers during the dry season; evidently, many people did not frequently clean their water-storing containers throughout the dry season. Secondly, the people in Lansaka District planted fruits (e.g. durians, mangosteens, and jackfruits) as their main occupation and some households in Khaokaew and Thadi subdistricts liked to water their fruits by placing a water container under their fruit tree, making it a key breeding site for *Ae. albopictus* to lay their eggs. Third, Thadi people preferred to keep a higher number of plant pots around their houses. Besides, the Thadi Administration Organisation does not provide rubbish/waste collection services in this subdistrict, and thus, Thadi people need to clean their

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rubbish/waste by themselves; they do so by burning their trash outdoors. During the dry season, it is easier for them to burn the waste more often compared to during the wet season, as rainwater makes the waste too wet to be burned. Fourth, Khaokaew people have the habit of using and throwing away a higher amount of refuse around their house.

Conclusions

Competitive interactions between *Ae. aegypti*, *Ae. albopictus* and *Culex* spp. in Southern Thailand are asymmetrical when they coexist in nature. The seasonal condition-specific competition is the mechanism contributing to species coexistence. With high competitive asymmetry, the competitive inferior species shift their temporal patterns to lower interspecific competition. During the wet season, when breeding sites are highly abundant, the majority of breeding sites are occupied with only *Ae. albopictus* larvae (superior competitor). In contrast, during the dry season when breeding sites become very scarce, inferior species (*Ae. aegypti* and *Culex* spp.) have no other choice but to lay eggs in containers where *Ae. albopictus* larvae already occupy.

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Conflict of Interest

The authors declare no conflict of interest.

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