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RESEARCH ARTICLE

Abundance of urban male mosquitoes by green infrastructure types: implications for landscape design and vector management

Gwendolyn K. L. Wong · C. Y. Jim

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Abstract
Context Urban green space (UGS) is widely espoused in sustainable urban design. Notwithstanding its ecosystem services, UGS is commonly perceived as inadvertent habitats for urban mosquitoes. Moreover, the lack of ecological understanding of mosquitoes and their urban habitats renders vector control in green spaces without reliance on chemical and bio-pesticides especially challenging.
Objectives This study envisages the application of a comparative analytical method for the evaluation and optimization of vector management in different urban spaces. The research examines the extent of male habitat preference as measured by population characteristics of urban adult mosquitoes on green roof and control sites.
Methods Adult mosquito traps were deployed on green roofs (GR), bare roofs (negative control, NC), and low-elevation gardens (positive control, PC). Distribution of male and female members of vector species were analyzed
Results Urban adult male mosquitoes exhibited highly-selective habitat use of the studied urban spaces, in that they were clustered chiefly in PC. Their spatial distributions are consistently explained by site group even under the stringent measure of presence/absence. The sex ratios of GR and NC were highly skewed toward females, which lends further to the interpretation of strong male habitat preference for the studied PC gardens.
Conclusions Urban mosquitoes do not display similar degrees of affinity for different types of green infrastructure. The methodology used can help prioritize urban sites and optimize control strategies. The uses of amenable environmental features salient to mosquito survival in landscape design should be explored as a sustainable and environmentally-friendly vector management approach.

Keywords Green roof · Urban green infrastructure · Urban green space · Urban mosquito · Urban habitat · Landscape management

G. K. L. Wong · C. Y. Jim (✉)
Department of Social Sciences, Education University of Hong Kong, Tai Po, Hong Kong SAR, China
e-mail: hragjcy@hku.hk

G. K. L. Wong
e-mail: gwendola@connect.hku.hk

Introduction

Urbanization and vector-borne diseases

Anthropophilic mosquito species have adapted to thrive in urban environment as pests. Beyond nuisance, infected mosquitoes can transmit disease-causing pathogens. Responsible for substantial human morbidity and mortality, vector-borne diseases cause more than one billion infection cases and claim a million related deaths yearly worldwide (WHO 2014).

As urban populations continue to expand, more humans become exposed to emerging and re-emerging mosquito-borne diseases. Massive urbanization has also generated settlements with high host densities and low predation stress, thereby increasing survival success for pests and transmission of pathogens. In the past two decades, a number of medically important vector-borne diseases have re-emerged or spread to new regions of the world (WHO 2014), including Zika and Japanese encephalitis.

Incessant global conveyance of people and goods also extend the geographical spread of vectors and pathogens well beyond their native range (Lounibos 2002; Hayden et al. 2010). Invasive species of tropical origin, such as *Aedes albopictus* and *Aedes aegypti*, have successfully established refuge in many temperate regions of the world (Medlock et al. 2012). Furthermore, changing weather and microclimate patterns, e.g., warmer urban microclimates, may enhance mosquito development and survival (Githeko et al. 2000).

The built environment engenders a distinctive and often novel set of urban habitats for mosquitoes, along with characteristic patterns, processes, and unintended functions. The growing human urban populations occupy and share the same living spaces with urban mosquitoes. Despite such close spatial proximity, the landscape ecology of urban vector mosquitoes remains largely nebulous.

Male mosquitoes and urban vector ecology

Mosquito surveillance studies have seldom focused on male mosquitoes as, unlike their female counterparts, they do not require blood-meals. Yet, the uneven attention is not conducive to developing a holistic understanding of the species in whole. From ecological perspectives, males play an indisputably important role in determining population dynamics, as reproduction requires both sexes. Moreover, male mosquitoes tend to swarm in groups at the mating arena (Oliva et al. 2014a, b). Location patterns of male–female encounters signify key target areas in vector management.

The life-cycle requirements of male mosquitoes are furnished by environmental resources (e.g. sugary substances; shelters). Male mosquitoes also utilize the same types of environmental resources as their female counterparts. The availability of such resources in the built environment constitutes functional habitats for urban mosquitoes. The few studies that had examined male catch have attributed high male abundance to the proximity of larval sources in the habitat (Unlu and Farajollahi 2014; Unlu et al. 2014). Altogether, the missing knowledge concerning male mosquitoes in urban ecology is crucial to the development of cost-effective vector intervention strategies, such as the optimization of timing and location (Esteva and Yang 2005; Lees et al. 2015). Therefore, the urban ecology of male mosquitoes, particularly in vegetated urban green spaces where much of the required resources are present, demands closer examination.

Urban green space and pest concerns

The importance of green space to the health of urban dwellers is increasingly realized in urban planning and design. Well-designed and distributed green spaces are pivotal to livable and sustainable cities (Gill et al. 2007). Urban green infrastructure (UGI) provides multiple ecosystem services to counteract the deleterious impacts of conventional built environment such as urban heat island effect. The salubrious contribution of UGI in the physical and mental health of humans can be gleaned from a confluence of experimental, epidemiological, and questionnaire studies (Tzoulas et al. 2007).

When land resource is limited, the allocation of green spaces may have to contend with alternative land-use and planning decisions (Tan and Hamid 2014). Green roofs, or living roofs, are specially designed landscaped roofs on buildings and structures. Compared to other UGIs, green roofs are especially versatile for compact cities as they do not occupy additional land area. Greening rooftops can deliver many services to building owners as well as the wider public, from urban heat island amelioration (Takebayashi and Moriyama 2007), stormwater mitigation (Wong and Jim 2014, 2015), air pollution abatement (Speak et al. 2012), building energy efficiency (Jim 2015), to aesthetic and amenity enhancement for the neighborhoods (Yuen and Wong 2005).

Notwithstanding the multitude of benefits, UGS is generally perceived to be accompanied by collateral unintentional “disservices” (Lyytimaki and Sipila 2009), such as habitat provision for urban pests like vector mosquitoes (Gomez-Baggethun et al. 2013).

Since vegetation indices are associated with mosquito presence (Brown et al. 2008; Hayden et al. 2010) and implicated in the transmission of vector-borne diseases (Ruiz et al. 2007, 2010), it is no surprise to find public negative attitudes and perceptions toward blue-green spaces like wetlands and riparian corridors (Dobbie and Green 2013; Vollmer et al. 2015). As a component of UGI, green roof is not exempted from this popular association. It has been reported that mosquitoes are among one of the residents' concerns regarding rooftop greening (Yuen and Wong 2005). However, research evidence on the actual affinity of urban mosquitoes for green roof and other UGIs remains scarce.

Study objectives

This study aims to evaluate the degree of preference of urban adult male mosquitoes for urban green spaces, particularly green roofs, as expressed in spatially-defined population characteristic measures. The experimental design covers concurrent mosquito surveillance on green roofs along with negative and positive control sites. To reduce potentially confounding regional population differences, the study sites were within a general active dispersal range of mosquitoes. We hypothesized site-group-specific heterogeneity in the spatial distribution of urban male mosquitoes between green roofs and control sites in the urban landscape. This study also envisages the application of this comparative analytical method to guide the evaluation and optimization of vector management in other urban spaces.

The second objective of this study is to reveal important patterns of urban vector ecology derived from the data that are relevant to mosquito control and management programs. Population characteristics have direct relevance to the design, optimization, and other important operational aspects of control strategies (Unlu et al. 2014). This study evaluated mosquito abundance (overall and by site group), adult sex ratio and its temporal and physical distribution across the study site groups, as well as male–female interaction. An additional measure of presence/absence was also analyzed to uncover more patterns from the data. Identifying patterns and processes in population dynamics can enhance our understanding of vector populations and integrated vector management.

Methods

Study setting

Hong Kong has a monsoon-driven humid-subtropical climate with relatively distinct seasonal variations—spring is usually warm and damp (around March to April), summer hot and wet with maximum daily temperatures often exceeding 31 °C (HKO 2003) (May to September); autumn warm and dry (mid-September to November); winter cool and dry.

Hong Kong is an important metropolis of China's Pearl River Delta (PRD) with a growing population of 7.37 million residing on 1104 km^2 of land (Census and Statistics Department 2017). Given its rugged topography, developments have to cluster in the limited costal and lowland areas. The compact development mode, adopted since the early development of the city in the 1840s, is characterized by densely-packed high-rise buildings and exceptionally high population density.

Land supply at the street level for urban green spaces has always been assigned sparingly, resulting in a grave shortage of this pertinent amenity in the city. The amount of public open space, at merely 2.9 m^2/capita, is probably one of the lowest in the world for cities of a comparable scale (Jim and Chan 2016). The low planning standard for public open space at 2 m^2/capita, which has remained unchanged for some eight decades, implies little prospect of allocating more land to meet rising demands. To find solution space, rooftops have been enlisted as alternative green sites mainly on government and institutional buildings with relatively large floor plate and low-rise design, and on podium tops of large high-rise residential developments (Tian and Jim 2011). These elevated green enclaves offer supplementary outdoor recreational venues in semi-private setting and convenient locations. As collateral ecosystem services, they serve as habitats to enhance urban biodiversity and stepping stones for wildlife to penetrate into the city.

As a city with a high volume of inbound and outbound visitors and goods, Hong Kong is susceptible to importing mosquito-borne pathogens from infected humans and vector mosquitoes. Such geographic mobility of infectious pathogens can result in the establishment and subsequently trigger secondary local transmission (Ma et al. 2011).

A university campus representative of the local urban form was selected as the study area (Fig. 1). The campus is comprised of a mixture of closely-spaced mid- to high-rise buildings for education and research purposes. It occupies the sloped lot between the densely-built urban core around the Victoria Harbour and the upslope and well wooded Lung Fu Shan Country Park.

Experimental design and equipment setup

With an aim to examine urban adult vector mosquitoes and green roofs, the study design incorporates three distinctively different types of urban environments as treatment and control sites—green roofs (GR), bare roofs as negative control sites (NC), and low-elevation green space as positive control (PC) (Table 1). Seven representative locations were identified from the campus based on criteria including suitability, accessibility, safety, and the availability of a weather-proof power source for the electrical mosquito trapping device (Fig. 1). In order to minimize other factors potentially contributed by regional (and presumably mosquito population) differences, the selected sites are within the general voluntary dispersal distance of mosquitoes (under 500 m). The locations of the sites are also fairly evenly distributed among treatment groups. Therefore, catch comparisons could reveal urban mosquito preference for the studied site groups.

The GR sites consist of three separate vegetated roofs on the highest level of their respective building. All green roofs are of the extensive type with herbaceous groundcovers growing in a relatively thin substrate layer. This popular green roof design demands low load-bearing capacity and little maintenance. Well-designed substrate and drainage layers allow fast shedding of excess rainwater to prevent stagnant water pools. Two of the sites contained flowering plants. The roof area and height of the buildings on which the studied green roofs are located are comparable to those generally found on government and institutional buildings elsewhere in Hong Kong. With regulatory control from the local building ordinance, the study sites' construction and material characteristics are similar to the local building profile.

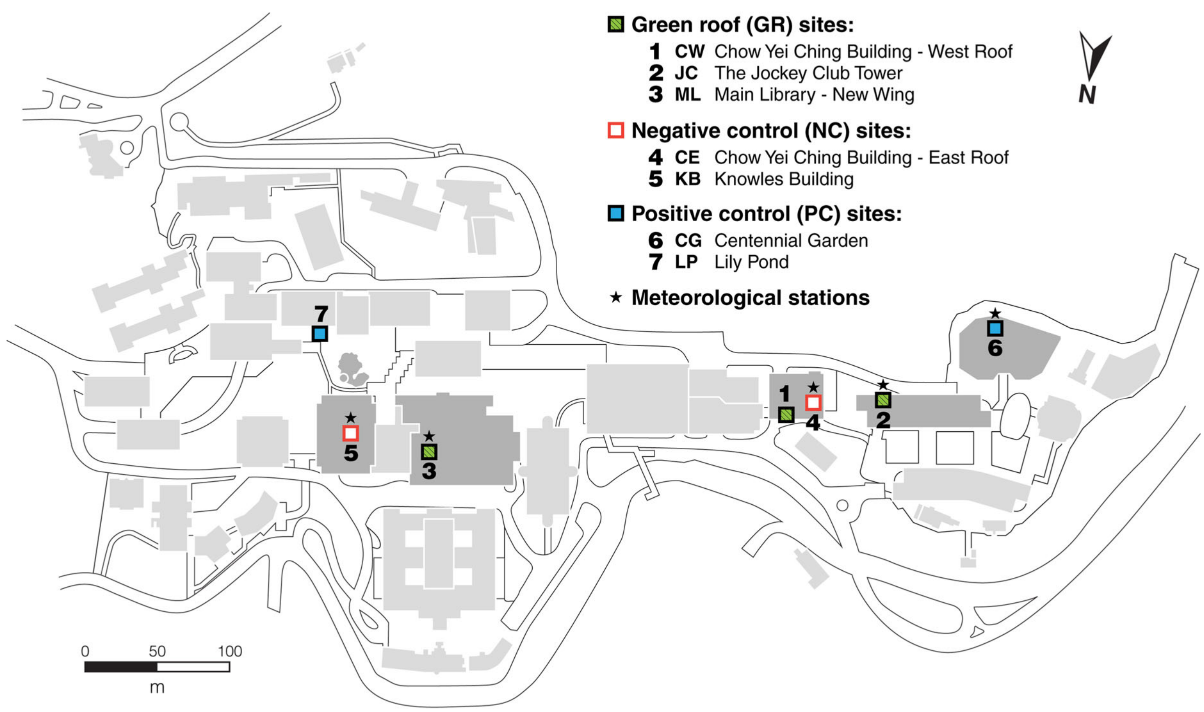


Fig. 1 Main campus map of the University of Hong Kong indicating locations of the seven experimental sites, five of which included a meteorological station, namely GR2, GR3, NC1, NC2 and PC2. Site notations and descriptions are provided in Table 1. The campus occupies a sloping ground descending from the south toward the north, above which are wooded hillslopes with some scattered residential blocks, and below which are densely developed residential and commercial areas along a harbor front

Table 1 Notations and pertinent characteristics of the experimental sites in the university campus

Group	Notation	Location	Elevation (m)	Total area (m^2)	Landscaped area (m^2)	Landscaped area (%)	Human traffic	Prominent vegetation growth forms	Presence of water body
GR	CW	Chow Yei Ching Building-West	123	91.1	73.4	80.6	Low	Grass, forbs	None
GR	JC[a]	Jockey Club Tower	144	1856.5	177.4	9.6	Medium	Shrubs, groundcovers, forbs	None
GR	ML[a]	Main Library-New Wing	100	2466.4	671.3	27.2	Medium	Groundcovers, grass, forbs	None
NC	CE[a]	Chow Yei Ching Building-East	123	583.7	0.0	0.0	Medium	None	None
NC	KB[a]	Knowles Building	107	1966.0	0.0	0.0	Low	None	None
PC	CG[a]	Centennial Garden	100	4391.0	3284.0	74.8	Medium	Trees, shrubs, grass, forbs	Disused water tanks; garden pond nearby
PC	LP	Lily Pond	85	1526.0	919.7	60.3	High	Trees, shrubs, aquatic plants	Ornamental garden pond

[a]Equipped with a weather station

The two NC sites are bare vacant roofs that serve as negative controls for the green-roof vegetation effect. The selection of gardens as PC sites were based on the authors' observation and local knowledge (i.e., frequent mosquito encounters). Nearby gardens were chosen as PCs to serve as a reference to the mosquito population on campus. The two PC sites are low-elevation gardens with great vegetated coverage and open water features. The low-elevation podium garden (CG) (Table 1) is accessible from the first floor of the campus buildings. Built on top of a district service reservoir structure against a steep slope, it surrounds a historic heritage water treatment plant with disused exposed filter beds that collect rainwater. Another PC garden (LP) features an ornamental pond with aquatic plants and fishes. Overall, group membership (GR, NC, and PC) encapsulates their idiosyncratic biophysical characteristics. The suitability of the site selections was also guided by their comparability with sites commonly found elsewhere locally. Data collected from NC and PC can thus provide useful baselines to assess the preference of adult mosquitoes for green roofs.

BG-Sentinel traps (Biogents Gmbh, Regensburg, Germany) which utilize air currents, olfactory, and visual cues as host signals were used to capture adult mosquitoes. Previous studies have shown the BG-Sentinel to be effective in capturing multiple mosquito species, including *Aedes* and *Culex* mosquitoes (Krockel et al. 2006; Farajollahi et al. 2009; Luhken and Kiel 2012; Fonseca et al. 2013; Azil et al. 2014; Unlu and Farajollahi 2014; Unlu et al. 2014) of male and female sex (Lacroix et al. 2009; Lees et al. 2014; Unlu et al. 2014). Since some target species are active during daytime (e.g., *Aedes albopictus*) while others are nocturnal (e.g., *Culex quinquefasciatus*), the traps operated continuously 24 h every day. Regular replacements of lure cartridges were made prior to the end of their service lives to ensure consistent scent emission across time and site locations.

Local vector mosquitoes

Hong Kong's humid subtropical climate provides favourable conditions for mosquitoes. Of the mosquito species found in the territory, some have established

Table 2 Major vector mosquito species recognized by the local government agency. *Sources* FEHD (2005), WHO (2014), ISSG (2015), ECDC (2016)

Species	Common name	Important infectious disease
Aedes aegypti[b]	Yellow fever mosquito	Chikungunya, dengue fever, West Nile virus, yellow fever, Zika
Aedes albopictus[a,b,c]	Asian tiger mosquito	Chikungunya, dengue fever, Japanese encephalitis, West Nile virus, yellow fever, etc.
Aedes japonicus[b]	Asian bush mosquito	Chikungunya, dengue fever, Japanese encephalitis, St Louis encephalitis, West Nile virus
Anopheles jeyporiensis[c]	–	Filariasis, malaria
Anopheles maculatus	–	Malaria
Anopheles minimus[c]	–	Malaria
Anopheles sinensis	–	Filariasis, malaria
Culex fuscocephala	–	Japanese encephalitis
Culex gelidus	–	Japanese encephalitis, West Nile virus
Culex quinquefasciatus[c]	Southern house mosquito	Filariasis, Japanese encephalitis, St Louis encephalitis, West Nile virus
Culex tritaeniorhynchus[c]	–	Filariasis, Japanese encephalitis

[a]Listed in the "Top 100" Global Invasive Species Database

[b]Listed in the Global Invasive Species Database

[c]Medically important mosquito species in Hong Kong

invasive status through a wide global distribution. Local government routine monitoring has recorded at least 72 species in the region, including the medically important genera of *Aedes*, *Anopheles*, and *Culex* (FEHD 2005). Among the 46 commonly spotted species, *Aedes albopictus*, *Anopheles jeyporiensis*, *Anopheles minimus*, *Culex quinquefasciatus*, and *Culex tritaeniorhynchus* recurred frequently. In Hong Kong the most reported mosquito-borne diseases in recent decades are dengue fever and Japanese encephalitis (FEHD 2005; Ma et al. 2011).

This study focuses on local mosquito species that are implicated or capable of carrying infectious pathogens. Eleven potential epidemic vector species were chosen based on government information (Table 2) (FEHD 2005), denoted hereinafter as "target species". Five target species are regarded as "medically important" by the local authority. Three target species are considered as "global invasive species" by the Invasive Species Specialist Group (ISSG) of the World Conservation Union (IUCN) Species Survival Commission, for their extensive global distribution and impact on biological diversity and/or human activities (ISSG 2015). The Asian tiger mosquito *Aedes albopictus* is among the "Top 100" in the ISSG Global Invasive Species Database. This aggressive vector has become an invasive species in at least 28 countries beyond its native range (Benedict et al. 2007; Ma et al. 2011).

Data collection and analyses

Pilot testing was conducted prior to data collection. Live data began in March 2015 and lasted for 52 weeks. Trapped mosquitoes were collected every fortnight, except the first two collection periods which were 15 and 13 days respectively due to conflict with a public holiday. Catch bags were reposed in a freezer prior to periodic identification under a stereomicroscope. The catch was sorted and counted by site and date. Identification was based on standard mosquito diagnostic keys and reference materials (Reuben et al. 1994; FEHD 2005; Becker et al. 2010). The sex and species of the mosquito targets (Table 2) can be determined by distinguishable morphological traits. Other mosquitoes and bycatch were recorded but not analyzed. The total percentage of unidentifiable damaged mosquitoes ($< 1\%$) was regarded as negligible.

Generalized Linear Models (GLIMs or GLMs) were used to evaluate the extent of the relationships between target-species abundance and site group. A negative binomial model with a logarithmic link function was selected as the suitable link for count data (Smithson and Merkle 2014). Inherent assumptions and autocorrelation were checked to ensure the absence of violation. Standard diagnostic tests were performed to evaluate model fit.

Based on the predictable swarming behavior of male mosquitoes in mating (Oliva et al. 2014a, b), a stringent measure—presence—was adopted to evaluate male–female interaction. The measure evaluates the effect of site group on urban male mosquitoes by using binary logistic regression (BLR) to examine the probability of dichotomous male presence (MP) as explained by site group. Male presence, compared with analyzing the number of male mosquito catch, offers a more conservative and stringent approach to determine whether differences in site preference exist between the three site groups. In this study, the presence of males belonging to the target vector species (MP), i.e., 1 = positive by presence; 0 = null by absence, serves as a dichotomous dependent variable. Site group (i.e., GR, NC, PC) serves as a categorical explanatory variable. Differences in MP between sites under concurrent mosquito trapping can reveal the contribution of site group. Species-specific analyses for local medically important species of greater pest/vector status (e.g., *Ae albopictus*) were also performed where appropriate. All statistical analyses were performed using IBM SPSS statistical software, Version 23.

Results

Overall male abundance and adult sex ratio

The monitoring period collected altogether 4477 mosquitoes of the target vector species, of which 2132 (47.6%) were male and 2345 (52.4%) were female urban adult mosquitoes. Expressed in male-to-female sex ratios (normalized to every 100 females), the overall sex ratios (all sites and periods combined) were 91:100 (all target species), 58:100 (*Ae. albopictus*), 100:100 (*Ae. japonicus*), and 80:100 (*Cx. quinquefasciatus*).

The temporal distribution of the target male mosquitoes mainly concentrated in warmer months. About 94% of the entire male mosquito catch was collected from April to November. *Ae. japonicus*, *Cx. quinquefasciatus*, and *Ae. albopictus* represented the vast majority of the catch (Fig. 2).

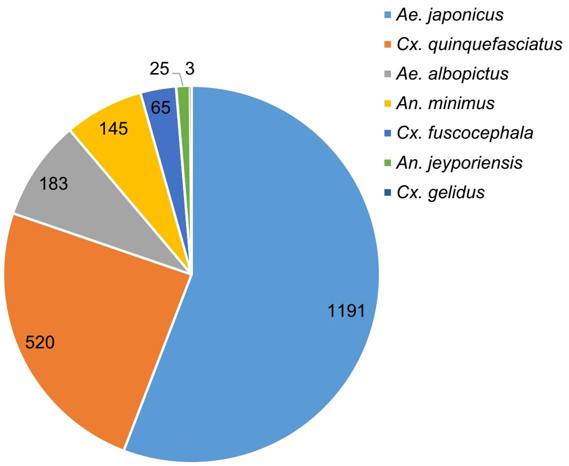
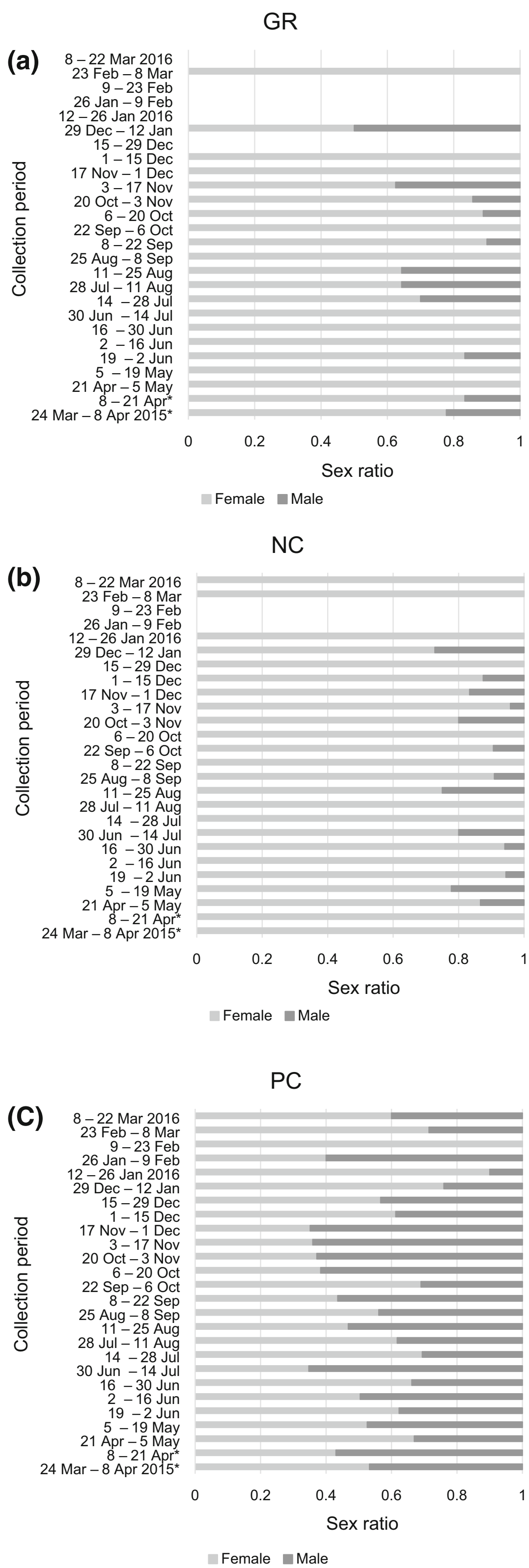


Fig. 2 Composition and abundance of all male members of the target mosquito species recorded during the study period. No male members were collected for four of the eleven target species (see Table 2)

Differences in sex ratios and male abundance between site groups

At the site-group level, the two sites in the PC group alone amassed 2085 males, almost 98% of the entire male catch. In comparison, 22 males were caught from the two NC sites and 25 from the three GR sites. Female abundance exhibited a similar pattern, although the magnitude of the difference was not as substantial—1957 female vectors were collected at PC sites (83.5%). The two NC and three GR sites had 224 and 164 female mosquitoes, respectively. Expressed in male-to-female sex ratios (normalized to every 100 females), the sex ratios were 107:100 in PC, 9:100 in NC, and 15:100 in GR.

The temporal distributions of the sex ratio of the three site groups are displayed in Fig. 3. In PC sites, males seem to represent greater share of the population toward the end of the active season (i.e., November) than in summer (around July–August). While the sex distribution in PC exhibited a relatively higher degree of evenness (i.e., comparable number of males to females) over the course of the monitoring period, the adult mosquito catch in NC and GR were consistently female-skewed. In other words, male abundance was steadily low on the rooftop sites compared with female abundance. The analyses below explore in greater



◀**Fig. 3** Sex ratio (light gray—female; dark gray—male) of **a** green roof (GR), **b** negative control (NC) sites, and **c** positive control (PC) over the span of the study period

detail the magnitude of the site-group differences observed.

The GLM on site group effect and male abundance was statistically significant ($df = 2$, $N = 182$) at the 0.001 level. Using PC as baseline for comparison, the relative abundance of GR is 99.5–98.6% less, while NC is 99.4–98.1% less (Table 3). Using GR as baseline, the relative abundance of PC is 125.1 times higher, and NC fell short of significance. As expected, ground-level blue-green spaces with relatively large open water bodies attracted the most adult male mosquitoes among our three experimental groups. Male abundance difference between the two rooftop sites—GR and NC—was insignificant.

At the species level, both male *Ae. albopictus* and *Ae. japonicus* exhibited similar site-preference pattern as the combined data (Table 3), although the preference of the former to PC using GR as baseline was not as high (i.e., 44.0 times instead of 125.1) as the species-combined model. For *Cx. quinquefasciatus*, the difference between NC and GR was significant at the $p < 0.01$ level. The relative abundance of male *Cx. quinquefasciatus* mosquitoes on NC is about five times greater than GR.

Differences in male presence between site groups

Site preference of urban adult male mosquitoes was further examined using male presence (MP) (0 = absence; 1 = presence). The percentages of biweekly collections with male presence in PC is substantially greater than the other site groups (Fig. 4).

Binary logistic regression (BLR) was conducted to assess whether our experimental site group alone can significantly explain the occurrence of mosquito male presence of all target species. The overall model was found to be statistically significant ($\chi^2 = 50.168$, $df = 2$, $N = 182$, $p < 0.001$). The Nagelkerke R^2 is 0.321, suggesting that by approximation about 32% of the variation in male presence can be explained by the model (Long 1997; Bewick, Cheek and Ball 2005). The predictive capacity of the model increased by about 20% from the null-hypothesis model (i.e., 51.6–71.4%). Thus, the

Table 3 Summary for generalized linear models (GLM) of site group and male abundance with positive control (PC) and green roof (GR) sites as baseline categories

Variable	*B*	*SE*	*p*	IRR	95% CI
All target mosquito species					
Site group					
GR	− 4.829	0.269	***	0.008	(0.005–0.014)
NC	− 4.551	0.291	***	0.011	(0.006–0.019)
(base = PC)					
PC	4.829	0.269	***	125.100	(73.793–212.080)
NC	0.278	0.343	NS	1.320	(0.674–2.584)
(base = GR)					
Aedes albopictus					
Site group					
GR	− 3.784	0.452	***	0.023	(0.009–0.055)
NC	− 5.170	1.022	***	0.006	(0.001–0.042)
(base = PC)					
PC	3.784	0.452	***	44.000	(18.139–106.730)
NC	− 1.386	1.095	NS	0.025	(0.029–2.137)
(base = GR)					
Aedes japonicus					
Site group					
GR	− 5.282	0.380	***	0.005	(0.002–0.011)
NC	− 7.074	1.020	***	0.001	(0.0001–0.006)
(base = PC)					
PC	5.282	0.380	***	196.833	(93.558–414.111)
NC	− 1.792	1.069	NS	0.167	(0.021–1.355)
(base = GR)					
Culex quinquefasciatus					
Site group					
GR	− 5.003	0.484	***	0.007	(0.003–0.017)
NC	− 3.262	0.305	***	0.038	(0.021–0.070)
(base = PC)					
PC	5.003	0.484	***	148.800	(57.648–384.077)
NC	1.740	0.534	**	5.700	(2.003–16.220)
(base = GR)					

NS not significant

$^{**}p < 0.01$

$^{***}p < 0.001$

incorporation of site group increased classification accuracy of the model. None of the Cook's D influence statistics was greater than one, indicating that no cases influenced the model unduly. Receiver operating characteristics (ROC) curve was generated as a diagnostic measure to examine the goodness-of-fit of the logistic model in terms of sensitivity and 1-specificity. The resulting curve is statistically significant, with fair to excellent discrimination (AUC = 0.744, $SE = 0.037$, 95% CI = 0.672–0.816, $p < 0.001$) (Peng and So 2002; Hosmer and Lemeshow 2005).

All site groups were significant predictors of male presence (Table 4). Using PC sites as the baseline category for comparison, the regression coefficients for GR and NC were significant and negative, suggesting associations with the decreased odds of male presence. Moreover, the odds ratios show that GR is 93.0% less likely to catch male mosquitoes of vector species than PC. Similarly, the odds for NC is 95.3% less likely to catch male mosquitoes than PC.

Using GR as the baseline category for comparison, only PC was a significant predictor ($p < 0.001$), while NC is statistically insignificant ($p > 0.05$) (Table 4).

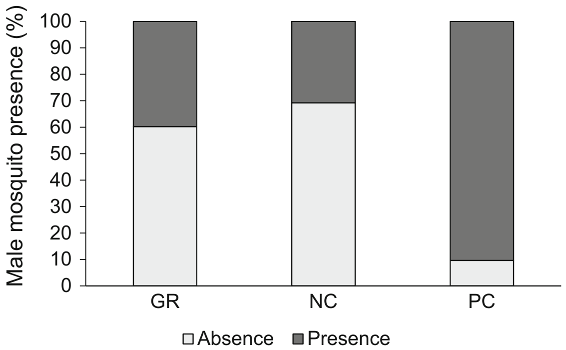


Fig. 4 Stacked bar graph showing the percentage of biweekly collections with male absence and presence of the three experimental groups. GR denotes green roof, NC negative control, and PC positive control groups

PC is associated with increased odds of male presence, with about 14 times more likely to catch male mosquitoes of vector species than GR. A separate BLR model with subset data containing only GR and NC sites was generated. As expected, the overall model was not significant ($N = 130$, $p > 0.05$). Therefore, the odds of catching males in NC sites is not significantly different from that of GR sites.

Species-specific BLR models for *Ae. albopictus*, *Ae. japonicus*, *Cx. quinquefasciatus* male presence and site groups were also evaluated (Table 4). The results largely correspond to those of the analyses on male abundance (Table 3).

Table 4 Summary for binary logistic regression (BLR) of site group and male presence with positive control (PC) and green roof (GR) sites as baseline categories

Variable	*B*	*SE*	*p*	OR	95% CI
All target mosquito species					
GR	− 2.657	0.524	***	0.070	(0.025–0.196)
NC	− 3.052	0.558	***	0.047	(0.016–0.141)
(base = PC)					
PC	2.657	0.524	***	14.252	(5.101–39.818)
NC	−0.395	0.379	NS	0.674	(0.320–1.417)
(base = GR)					
Aedes albopictus					
GR	− 2.874	0.510	***	0.056	(0.021–0.153)
NC	− 4.321	1.049	***	0.013	(0.002–0.104)
(base = PC)					
PC	2.874	0.510	***	17.714	(6.515–48.163)
NC	− 1.447	1.096	NS	0.235	(0.027–2.014)
(base = GR)					
Aedes japonicus					
GR	− 2.787	0.488	***	0.062	(0.024–0.160)
NC	− 4.402	1.049	***	0.012	(0.002–0.096)
(base = PC)					
PC	2.787	0.488	***	16.229	(6.235–42.238)
NC	− 1.615	1.085	NS	0.199	(0.024–1.667)
(base = GR)					
Culex quinquefasciatus					
GR	−3.916	0.601	***	0.020	(0.006–0.065)
NC	− 2.097	0.448	***	0.123	(0.051–0.295)
(base = PC)					
PC	3.916	0.601	***	50.214	(15.460–163.095)
NC	1.819	0.605	**	6.167	(1.884–20.187)
(base = GR)					

NS not significant
**$p < 0.01$
***$p < 0.001$

Classifying male abundance and presence using female data

The interaction between males and females was further evaluated using GLM. The model with female abundance as the contributing factor to male abundance was statistically significant ($df = 1$, $N = 182$, $p < 0.001$). Female abundance exhibited a positive relationship with male abundance ($B = 0.067$, $p < 0.001$). A unit of increase in female abundance corresponds to 6.9% increase (95% CI 1.060–1.079) in their male counterpart.

Female presence was generated to compare its interaction with male presence using BLR. The resulting model was significant ($\chi^2 = 43.989$, $df = 1$, $N = 182$, $p < 0.001$). The Nagelkerke R^2 was 0.286. The classification accuracy of the model increased by about 16.5% from the null-hypothesis model (i.e., 51.6–68.1%) after incorporating site group. The odds of male presence predicted by the model was 50.6 times higher for female presence than absence.

The univariate analysis also allows for the conversion of odds to probabilities. The model indicated the probability of female presence to be 62% more likely to indicate male presence than were female absence (3%). With the decision rule threshold set at 0.5, 98.9% of collections with female presence predicting male presence (i.e., sensitivity) was correctly classified. The specificity of the regression was 35.2%, with 38.0% false positive and 3.1% false negative.

Discussion

Abundance of urban male mosquitoes by green infrastructure types

Using an urban green infrastructure framework to define treatment groups, our results reveal urban adult male mosquitoes' highly-selective habitat use of the studied urban space groups. The bulk majority of males were captured in low-elevation gardens, leaving green roof and bare rooftop sites highly female-skewed. This spatial clustering is consistently explained by site group in both measures—male mosquito abundance and presence. On the other hand, GR and NC had no difference in the species-combined dataset. Thus, contrary to the common oversimplification of green spaces as mosquito habitats, we provide evidence that urban mosquitoes do not display similar degrees of affinity for different types of green infrastructure.

The stark site-group contrast may be ascribed to microclimate and resource availability in the respective urban habitat. Previous study has identified higher wind speeds on rooftops as the microclimatic factor that explained the complementary female abundance data (Wong and Jim 2017). Other researchers have also attributed greater male abundance in urban areas to the availability of larval sites (Unlu and Farajollahi 2014; Unlu et al. 2014). Male mosquitoes would inarguably utilize their physical surroundings to maximize survival and reproductive success. The PC sites may have exhibited a number of favorable attributes toward such goals—site of adult emergence, proximity to larval sites, abundance of sugary foods and female mates—thus negating the need to engage in energy-intensive and risk-laden active dispersal to nearby green spaces.

Similar to the female catch (Wong and Jim 2016), *Ae. japonicus*, *Cx. quinquefasciatus*, and *Ae. albopictus* constituted the vast majority of the catch. These species are known to thrive well in urban environments (Medlock et al. 2006; Schaffner et al. 2011). Since *Ae. albopictus* and *Ae. japonicus* are listed as global invasive species, our findings may provide useful references to other regions. At the species-specific level, the relative abundance of male *Cx. quinquefasciatus* mosquitoes on bare rooftops is about five times greater than on green roofs. This interesting finding complements the slightly higher female abundance found on bare roofs than green roofs (Wong and Jim 2016, 2017). This pattern may be attributed to the collection of rainwater in roof-floor depressions due to weathering and uneven tile laying of elevated subtropical rooftops. In contrast, water pools are rarely present on green roofs due to the well-drained soil in conjunction with an efficient subsurface drainage layer. It also demonstrates the relatively stronger dispersal ability of the *Cx. quinquefasciatus* compared to the other captured species.

Male mosquitoes in urban vector ecology

Female mosquitoes have traditionally been the subject of interest in mosquito field studies (Unlu et al. 2014; Vanickova et al. 2017). Our yearlong concurrent-surveillance study examined population characteristics of urban adult male mosquitoes of vector species, including their abundance, adult sex ratio, temporal and physical distribution, and male–female interaction. Identifying patterns and processes in mating systems and population dynamics can improve our understanding of the vector populations, with useful implications for vector management approaches that target specific aspects of mosquito biology.

The data also shed light on the interaction between male and female populations. Abundance data revealed that males are positively related to females. The more stringent analyses on mosquito presence further elaborate that male presence is largely concurrent with the presence of female. In other words, males were rarely collected from a site without females. The swarming behavior of sexually mature males (Oliva et al. 2014a, b) has likely contributed to the dichotomous characteristic of the data (either present or absent). The results illustrate a close link between males and females in the wild population, and the potential value of information derived from male mosquito studies. Overall, the proclivity of male and female clustering at the community mating site makes such a preferred habitat of greater scientific interest for surveillance and control purposes (Lees et al. 2014).

Ecological implications for landscape design and vector management

Spatial distribution of urban mosquitoes and environmental resources

The spatial distribution of pests is an important consideration in formulating control strategies, particularly for spatially-biased pests with limited mobility like mosquitoes (Ikegawa and Himuro 2017). Prolific urban mosquito habitats signify important target management areas for priority intervention. In the male-manipulated biological control of mosquitoes, adult sex ratio reveals an additional level of information, in which the degree of potential competition between released and wild male mosquitoes can be assessed through the number of wild adult females available in the population of a given area (Boyer et al. 2011). Prior studies on wild adult mosquito sex ratio are rather limited. Nonetheless, our figures are comparable to those reported (between 1:2 and 1:1) for *Ae. albopictus* in other surveillance studies using similar device mechanisms (Lacroix et al. 2009; Unlu et al. 2014). It is believed that the operational sex ratio is highly male-skewed in mating site (Lees et al. 2014). The consistent differences between PC and rooftop sites (Fig. 3) suggest that the studied urban mosquito population utilized the former as the site of copulation instead of the latter. Thus, sites with higher male-to-female ratios may receive a higher priority in surveillance and vector control as part of public health management (Ferraguti et al. 2016).

The identification of important urban mosquito habitats, such as the community mating arena, also allows for closer examination of the types and qualities of environmental resources that are salient to mosquito survival in urban habitats. By actively incorporating ecological knowledge and principles, landscape planning and design can be informed, through a more systematic understanding, of the relationships between built environment and urban mosquitoes. Landscape design should take into consideration the potential spatial clustering of mosquito resources. Modification and removal of environmental resources can reduce the overall habitat quality for urban pest mosquitoes.

Temporal distribution of urban mosquitoes and environmental resources

Male mosquito abundance is also directly relevant to the design and operational aspects of male-manipulated control strategies. The number of released males cannot be determined arbitrarily without sound knowledge of the target populations. Male abundance is one of the major components in mosquito population model in simulations for evaluating and optimizing control strategy (Anguelov et al. 2012). Effective male-manipulated controls demand information on the threshold level of released males (Esteva and Yang 2005). Abundance patterns of the study community, e.g., temporal characteristics, can be gleaned from the type of data collected using our methodology. In our context, the majority of the mosquito catch occurred in the warmer summer months. This demonstrates the need to delineate periods when mosquitoes are active to coordinate the timing of treated-male release. Real-world data may be combined with computational approaches to determine the optimal timing and cost-effectiveness of control strategies.

The temporal aspects of mosquito resource availability (e.g. periods with sugary substances and emergence of aquatic oviposition sites from rainfall) should also be considered in landscape design. For example, it has been shown that female survivorship is positively associated with nectar-rich environments (Ebrahimi et al. 2017). Reducing sugar availability and accessibility in potential high-risk areas may be a useful strategy. Using design elements to promote asynchronous resource availability can also reduce the habitat quality for pest mosquitoes.

Methodological contributions and limitations

The comparative analytical methodology used in this study can be adopted for the evaluation and identification of management areas. The framework of urban green infrastructure can be enlisted to help identify priority sites for integrated pest management. Future study designs can be extended to compare other sets of green and non-green urban spaces. The results of this research warrants further studies be replicated in other settings and regional contexts (e.g., different mosquito species composition) such that a meta-analytic framework of urban vector ecology can be elaborated. Further analyses can also be performed to incorporate finer-scale urban habitat metrics and characteristics, such as habitat size (Skaff and Cheruvelil 2016; Talaga et al. 2017). Our study sites exhibit typical low-elevation gardens with open water features, green and grey roofs in the current local context. Future research may study other variations that are meaningful given their geographic and urban contexts (e.g. gardens without open water features; large city parks; green roofs on large shopping malls or on high-rise skyscrapers).

Applying ecological principles to landscape design and management

We hereby propose the use of ecological principles in mosquito-sensitive urban design (MSUD) as best management practices. The identification of mosquito-preferred habitats illustrates the prospects of minimizing favorable environmental attributes early in the planning and management processes. Knowledge from applied ecology can serve as valuable tools in urban planning (Gaston et al. 2013). Ecologically-informed decisions can be made in relation to amendable environmental features that are salient to mosquito survival. Concomitant with inputs from rigorous vector surveillance and locally relevant research, the proposed mosquito-sensitive approach may well contribute toward the sustainability of integrated vector management programs.

Conclusion

Urban mosquitoes display heterogeneous spatial distribution in the built environment characterized by green infrastructure type. The findings provide support that elevated green roofs are not particularly favoured by such pests. The data suggest that different types of urban green infrastructure may be associated with varying degrees of habitat-use depending on habitat quality and resource availability. Adopting a comparative methodology for site evaluation can help prioritize urban spaces for vector management. Information on target male mosquito populations is fundamental in the successful design and operation of emerging male-manipulated vector control strategies. A firm understanding of urban mosquito ecology can ensure the cost-effectiveness of such control strategies and inform evidence-based vector management policies.

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Author contributions GKLW and CYJ conceived and designed the research. GKLW performed the collection and analyses of data, and wrote the manuscript. GKLW and CYJ discussed the research findings and implications. All authors polished and approved the final manuscript.

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