

1 Quantification of human-mosquito contact rate using surveys and
2 its application in determining dengue viral transmission risk

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17 **Abstract**

18 *Aedes*-borne viral diseases, including dengue fever, chikungunya, and Zika, have been
19 surging in incidence and spreading to new areas where their mosquito vectors thrive. To estimate
20 viral transmission risks, availability of accurate local transmission parameters is essential. One of
21 the most important parameters to determine infection risk is the human-mosquito contact rate.
22 However, this rate has rarely been characterized due to the lack of a feasible research method. In
23 this study, human-mosquito contact rates were evaluated in two study sites within the Greater
24 New Orleans Region by asking a group of survey participants to estimate mosquito bites they
25 experienced in the past 24 hours. The fraction of the mosquito bites attributed to *Ae. aegypti* or
26 *Ae. albopictus* was estimated by human landing sampling. The results showed a significantly
27 higher outdoor mosquito bite exposure than indoor exposure. The number of reported mosquito
28 bites was positively correlated with the time that study participants spent outside during at-risk
29 periods. There was also a significant effect of the study site on outdoor bite exposure, possibly
30 because of the difference in the numbers of host-seeking mosquitoes. We use a mathematical
31 dengue virus transmission model to estimate the transmission risks in the study areas based on
32 local conditions. This compartmental model demonstrated how the observed difference in the
33 human-*Aedes* contact rates in the two study sites would result in differential dengue transmission
34 risks. This study highlights the practicality of using a survey to estimate human-mosquito contact
35 rates and serves as a basis for future evaluations. Combined with the use of mathematical
36 modeling, this innovative method may lead to more effective mosquito-borne pathogen
37 prevention and control.

38 **Author summary**

39 Even though the human-mosquito contact rate is among the most important indicators of
40 mosquito-borne viral transmission risk, it is rarely characterized in the field. Human Landing
41 Capture is a gold standard method to quantify this rate, but it ignores variables such as human
42 behaviors and lifestyles. In this study, we tested the feasibility of using surveys to quantify
43 mosquito bite exposure in the Southern United States. The survey results, combined with
44 mosquito species proportion data, were used to estimate the contact rate. These rates are key
45 parameters used in mathematical models to determine transmission risks. We found that bite
46 exposure occurred more often outside homes and people who spent more time outdoors in the
47 evening and night had a higher exposure. Our model analysis shows that the human-mosquito
48 contact rate is one of the most important parameters determining outbreak potential. Disease
49 control programs should focus their efforts on reducing this rate in addition to the mosquito
50 density. Future studies should test if the entomological contact rates described by surveys
51 correlate with disease incidences or other entomological indices. This study highlights the
52 importance of characterizing how vector-human contact rates may respond to changing human
53 behaviors and environments.

54 **Introduction**

55 Globally, mosquito-borne viral diseases are on the rise. In the past few decades, diseases
56 such as dengue, West Nile fever, chikungunya, and Zika have emerged and persisted in the parts
57 of the world where their mosquito vectors thrive [1-5]. It has been estimated that hundreds of
58 thousands of people die from mosquito-borne diseases each year [6]. Population growth,
59 unplanned urbanization, global warming, intercontinental travel, and the breakdown of mosquito
60 control infrastructure have all contributed to the expansion of mosquito vectors in multiple
61 locations throughout the world [7-11].

62 Dengue fever is the most common and widespread mosquito-borne viral disease in the
63 world [12]. According to a recent study [13] about 390 million dengue viral infections occurred in
64 2010, higher than the 50-100 million previously estimated by the World Health Organization.
65 Four serotypes of dengue virus (DENV) can be transmitted by two species of mosquito vectors in
66 the genus *Aedes*: *Aedes aegypti* (Linnaeus), the Yellow Fever mosquito, and *Aedes albopictus*
67 (Skuse), the Asian Tiger mosquito [14]. Both species are highly anthropophilic [1]. They are
68 widespread in residential settings of tropical and sub-tropical parts of Asia, Latin America,
69 Africa, and the Pacific [15]. Because of a suitably warming climate and the availability of larval
70 habitats, both *Aedes* species have gained a foothold in the Southern United States and Southern
71 Europe [16-18]. This, in combination with increases in international travel, results in a possibility
72 that DENV may emerge in these areas.

73 Mathematical models can help guide the design of effective preemptive and ongoing
74 disease control programs [19]. For these models to be effective, they require accurate estimates of
75 local transmission parameter values. One of the most important parameters determining pathogen
76 transmission is the human-mosquito contact rate, which we define as the total number of times
77 humans are bitten by mosquitoes each day in the area of interest [20]. Unfortunately, these rates
78 are rarely characterized because of the lack of appropriate research methods. The paucity of

79 contact rate data hinders our progress in understanding how changing environments and human
80 behaviors will affect mosquito-borne virus transmission and emergence. We need to know how
81 often, and under what circumstances, humans are exposed to mosquito bites to plan effective
82 mitigation strategies.

83 To date, only a few approaches have been used to approximate contact patterns in the
84 field. Human Landing Capture (HLC) is the traditional gold standard method to monitor human-
85 vector contact patterns in malaria transmission [21,22]. This method involves human volunteers
86 collecting mosquitoes that land on them to feed, typically at night when *Anopheles* spp., the
87 vectors transmitting malaria, seek a blood meal. A well-designed HLC study could potentially
88 approximate the contact rate when humans are bitten by mosquitoes while sleeping. However,
89 because *Aedes* spp. bite during the day when humans could actively interrupt or avoid mosquito
90 bites, this could result in a potential bias for the HLC estimates. The contact rate depends heavily
91 on housing infrastructure, human behaviors, and lifestyle differences that cannot be captured
92 easily by an HLC experiment [23-25].

93 In this study, we approximated the contact rates between *Aedes* spp. and humans in the
94 Greater New Orleans Region using a questionnaire-based survey and a small-scale HLC
95 experiment. A short questionnaire in the form of door hangers was used to ask research
96 participants about the frequency and location of mosquito bite exposures in the past 24 hours. An
97 HLC study was performed to determine the proportion of mosquito bites that belong to either *Ae.*
98 *aegypti* or *Ae. albopictus*. Next, the contact rates between humans and the *Aedes* species were
99 calculated. Finally, a deterministic compartmental SEIR (Susceptible, Exposed, Infected,
100 Recovered) model describing DENV transmission by *Ae. aegypti* and *Ae. albopictus* was used to
101 compare how the model predictions depend on the locally characterized human-mosquito contact
102 rates from two distinct locations.

103 The ultimate goals of this study were: 1) to test the feasibility of using questionnaire-
104 based surveys to quantify human-mosquito contact rates, 2) to understand how environmental

105 factors and human behaviors may impact mosquito bite exposure, and 3) to model how changes
106 in human-mosquito contact rates impact pathogen transmission outcomes.

107

108 **Methods**

109 **Study sites and survey methods**

110 We designed two questionnaires in the form of door hangers. We intentionally designed
111 short questionnaires to encourage participation. The first questionnaire (Supplementary Data 1)
112 was used in a preliminary survey to explore the range of bite exposure and to estimate the return
113 rate. The research participants were asked to indicate the number of mosquito bites they received
114 within the past 7 days, the locations in which they experienced mosquito bites most often, and the
115 frequency of mosquito bite exposures inside homes. All questions in this questionnaire were in a
116 multiple-choice format.

117 The second questionnaire (Supplementary Data 2) was designed after the preliminary
118 survey. The questions included open-ended questions inquiring about the amount of mosquito
119 bites participants received both indoors and outdoors, where they had received the outdoor bites,
120 and the time spent outside in the past 24 hours. The questionnaire also collected demographic
121 data including age range, gender, and number of people in their household.

122 In the preliminary survey, the questionnaires were distributed in August and September
123 of 2016 in three study sites: the Bywater and 7th Ward neighborhoods of Orleans Parish (ORL),
124 the Bridge City neighborhood of Jefferson Parish (JEF), and the Oak Harbor and Eden Isle
125 neighborhoods of St. Tammany Parish (TAM). Four street blocks were randomly chosen per
126 month from each of the three study sites. The questionnaires were distributed to all addresses in
127 the chosen blocks and collected back the next day.

128 In the second survey, only two study sites, ORL and TAM, were included. The study
129 period was from April to August 2017. In each month, 4 street blocks from each study site were

130 randomly selected, without replacement, to receive the questionnaires on Sundays, and another 4
131 blocks on either Wednesdays or Thursdays. The questionnaires were distributed to all addresses
132 in the chosen blocks and retrieved back the next day. No identifying information or addresses
133 were collected from the study subjects, and the Tulane University's Internal Review Board (IRB)
134 approved the full-review exempt status of both surveys (IRB reference number: 16-923467E).

135 The ORL site was in an urban environment close to New Orleans city's downtown area.
136 Compared to the other two study sites, ORL's residents were younger and lived in a smaller
137 household (almost 40% of all households were a 1-person household; US 2010 Census). Its
138 population median age was 38 (40 in JEF, and 50 in TAM; US 2010 Census). ORL was a racially
139 mixed neighborhood (52.85% African American and 41.86% White; US 2010 Census). JEF and
140 TAM are located further away from the city's downtown area in a more sub-urban environment.
141 TAM had the highest average household income (\$96,415; 2016 ACS 5-year estimates)
142 compared to ORL (\$55,709), and JEF (\$49,928). TAM also had the highest percentage of
143 households that were classified as "Family Household" (76.40%; US 2010 census). Racial
144 diversity was lowest in TAM (89.18% of total population were White). The population variables
145 of the study sites are shown in detail in Supplementary Table 1.

146 **Human Landing Catch (HLC)**

147 HLC experiments were performed in ORL and TAM to investigate the species
148 composition of host seeking mosquitoes from April to August 2017. Two locations were chosen
149 from each study site. In each location and month, HLC was performed once in the morning and
150 once in the evening on two separate days. Each collection consisted of two 45-minute capturing
151 sessions with an up to 15 minute break in between. The morning collection started within 30
152 minutes after sunrise, and the evening collection stopped within 30 minutes before sunset. The
153 HLC locations were shaded outdoor areas. The collector was seated on a chair with the legs
154 exposed from the shoes up to the knees, and the lower arms were exposed from the elbows down.

155 Collection of landing mosquitoes from the collector's own body was done using a portable
156 aspirator and the mosquitoes were either identified on site, when possible, or transported back to
157 the laboratory for further identification using a microscope. A single collector took part in all the
158 HLC sessions.

159 **Survey and HLC data analysis and statistical tests**

160 Because the first survey was a preliminary data collection with a small sample size, only
161 the data from the second survey was analyzed with statistical tests. In the second survey, the
162 sampling method was a two-stage stratified cluster sampling. To account for the differential
163 probabilities of selection due to the study design and to ensure more accurate estimates, a
164 sampling weight for each participant was calculated based on the selection probability
165 proportional to size. The population cohort was defined as persons aged >18 years old who lived
166 in the two study sites at the time of sampling. The Primary Sampling Unit (PSU) was at a
167 residential block level. The sampling probability of each block was $1/B_i$, where B_i is the total
168 number of blocks in study site i . The Secondary Sampling Unit (SSU) was at the research
169 participant level. The probability that a person in each household was selected was $1/P_j$, where P_j
170 was the household size for address j .

171 All data analysis was done using R (version 3.3.3) and R studio. The data and weights
172 were defined to create a Survey Object using Survey package [26]. Sampling weight for each data
173 point was calculated as the inverse of the probability of selection. Specifically, weight for each
174 data point was equal to $(1/B_i + 1/P_j)^{-1}$. All statistical tests downstream of the weighting procedure
175 were analyzed with the functions within Survey package. To compare the numbers of reported
176 bites and the time spent outside within the past 24 hours between groups, Wilcoxon Rank Sum
177 tests were used. Spearman's correlation tests were used to determine the correlation between the
178 time spent outside at each time interval and the numbers of reported bites received outdoors.

179 Two generalized linear models assuming quasi-Poisson distribution as the probability
180 distribution function of the response variable, with log link function, were created to analyze the
181 data. The first model used the total time spent outside between 5 pm to 6 am (evening and
182 nighttime) as a response variable. In this model, the independent variables included the age range
183 and gender of research participants, weekend/weekday setting, and study sites. The second model
184 used numbers of reported bites received outdoors within the past 24 hours as a response variable.
185 The independent variables included in this model were the time spent outside within the past 24
186 hours, the gender of research participants, the month of data collection, and the weekend/weekday
187 setting.

188 For HLC data analysis, comparisons between the numbers of landed *Ae. aegypti* or *Ae.*
189 *albopictus* between study sites and between times of collection were determined using the
190 Wilcoxon Rank Sum test. The proportions of *Ae. aegypti* and *Ae. albopictus* from HLC were
191 calculated based on average values of landing mosquito types across all HLC sessions for both
192 study sites.

193 **Dengue epidemiological compartmental model description and assumption**

194 Our compartmental mathematical model described the transmission of one serotype of
195 DENV by both vector species: *Ae. aegypti* and *Ae. albopictus*. We used this model to estimate
196 and predict quantities of interest at the initial epidemic spread. This model was adapted from a
197 mathematical mosquito-borne disease model published in a study by Manore *et al.* [20]. The
198 human-mosquito contact rates used in the model were based on the local survey data. We defined
199 human-mosquito contact rate (B) as the number of biting events that occurred by all mosquitoes
200 of a given species on the human population in the area of interest within a 24-hour period. In
201 other words, it was the number of bites all humans in the area of interest received from that
202 mosquito species within 24 hours. Note that we defined the mosquito's *biting rate* as a *per capita*

203 rate of bites that a typical single mosquito may give to humans per unit time. As a result, a
204 mosquito's biting rate was different from a human-mosquito contact rate.

205 The human population was divided into 4 compartments: susceptible (S_h), exposed (E_h),
206 infectious (I_h), and recovered/immune (R_h). The *Ae. aegypti* mosquito population was divided into
207 3 compartments: susceptible (S_g), exposed (E_g), and infectious (I_g). The *Ae. albopictus* mosquito
208 population was also divided into 3 compartments: susceptible (S_b), exposed (E_b), and infectious
209 (I_b). The total population sizes for *Ae. aegypti*, *Ae. albopictus* and humans were $N_g = S_g + E_g + I_g$,
210 $N_b = S_b + E_b + I_b$, and $N_h = S_h + E_h + I_h + R_h$, respectively. We assumed that the two vector species
211 do not interact. This means, for example, that the carrying capacities of the two species were
212 independent from each other. Supplementary Figure 1 shows a diagram of the model including
213 the relationship among all population compartments.

214 Humans entered the susceptible class S_h with a per capita birth rate Ψ_h . Humans were
215 bitten by *Ae. aegypti* with a rate of B_g/N_h (bites per person per day) or by *Ae. albopictus* with a
216 rate of B_b/N_h . These biting *Ae. aegypti* or *Ae. albopictus* had a probability of I_g/N_g , or I_b/N_b , of
217 being infectious, respectively. If a mosquito was infectious, then there was a probability of β_h that
218 the person will become infected. When a human was infected, they moved from susceptible class
219 S_h to the exposed class E_h . After an average intrinsic incubation period of $1/v_h$ days, they moved
220 to the infectious class I_h . Humans in the infectious class can infect other mosquitoes upon
221 contacts. After an average recovery time $1/\gamma_h$ days, the infectious humans recovered and moved to
222 class R_h . Recovered persons were assumed to have immunity to the infecting DENV serotype for
223 the entire period of the simulation. In addition, humans of all status left the population through a
224 per capita natural death rate μ_h . The death rate due to disease was assumed to be very low and
225 negligible. The human population size was assumed to be stable ($\Psi_h = \mu_h$), and migration of
226 mosquitoes and humans was low and negligible.

227 When a susceptible *Ae. aegypti* mosquito bit humans at a biting rate of B_g/N_g (bites per
228 mosquito per day), there was a probability I_h/N_h that the persons being bitten were infectious. If

229 the person was infectious, then the biting *Ae. aegypti* mosquito in the class S_g became infected
230 with a probability β_g and moved to the exposed class E_g . After an average extrinsic incubation
231 period $1/\nu_g$ days, the mosquito advanced to the infectious class I_g . Similarly, when a susceptible
232 *Ae. albopictus* mosquito bit humans at a biting rate of B_b/N_b , there is a probability I_h/N_h that the
233 persons were infectious and a probability β_b that the mosquito became infected and advanced to
234 the exposed class E_b . After an extrinsic incubation period $1/\nu_b$ days, the *Ae. albopictus* mosquito
235 advanced to the infectious class I_b . Both mosquito species remained infectious for life.

236 Female mosquitoes entered the susceptible class through recruitment from the pupal
237 stage. The recruitment term for mosquitoes was proportional to the egg-laying rate of adult
238 female mosquitoes and accounted for the hatching rate of eggs and survival of larvae and pupae.
239 The aquatic stages were not explicitly included in the model and were approximated by a density-
240 dependent recruitment (birth) rate. We assumed that all adult female *Ae. aegypti* and *Ae.*
241 *albopictus* mosquitoes had the same per capita natural death rate μ_g and μ_b , respectively. In this
242 model, dengue infection did not affect the mosquito death rate or biting rate.

243 **Model equations**

244 Our ordinary differential compartmental equations modeling dengue transmission were:

$$245 \quad \frac{dS_h}{dt} = \Psi_h H_0 - \lambda_h S_h - \mu_h S_h \quad (1a)$$

$$246 \quad \frac{dE_h}{dt} = \lambda_h S_h - \nu_h E_h - \mu_h E_h \quad (1b)$$

$$247 \quad \frac{dI_h}{dt} = \nu_h E_h - \gamma_h I_h - \mu_h I_h \quad (1c)$$

$$248 \quad \frac{dR_h}{dt} = \gamma_h I_h - \mu_h R_h \quad (1d)$$

$$249 \quad \frac{dS_g}{dt} = \eta_g N_g - \lambda_g S_g - \mu_g S_g \quad (1e)$$

$$250 \quad \frac{dE_g}{dt} = \lambda_g S_g - \nu_g E_g - \mu_g E_g \quad (1f)$$

$$251 \quad \frac{dI_g}{dt} = \nu_g E_g - \mu_g I_g \quad (1g)$$

$$252 \quad \frac{dS_b}{dt} = \eta_b N_b - \lambda_b S_b - \mu_b S_b \quad (1h)$$

$$253 \quad \frac{dE_b}{dt} = \lambda_b S_b - \nu_b E_b - \mu_b E_b \quad (1i)$$

$$254 \quad \frac{dI_b}{dt} = \nu_b E_b - \mu_b I_b \quad (1j)$$

255 The female *Ae. aegypti* and *Ae. albopictus* recruitment rates were:

$$256 \quad \eta_g = \psi_g - r_g \frac{N_g}{K_g} \quad (2)$$

257 and

$$258 \quad \eta_b = \psi_b - r_b \frac{N_b}{K_b} \quad (3)$$

259 Here, Ψ_g and Ψ_b were the per capita natural birth rates of female *Ae. aegypti* and *Ae.*
 260 *albopictus*, respectively. In the absence of density dependence, r_g and r_b were the intrinsic growth
 261 rates of female *Ae. aegypti* and *Ae. albopictus*, respectively, where $r_g = \Psi_g - \mu_g$ and $r_b = \Psi_b - \mu_b$.
 262 K_g and K_b were the carrying capacity of the female *Ae. aegypti* and *Ae. albopictus*, respectively,
 263 in the area of interest.

264 The force of infection from mosquitoes to humans (λ_h) was the product of the average
 265 number of bites a person received from mosquitoes per day (B_g/N_h and B_b/N_h), the probability
 266 that the mosquito was infectious (I_g/N_g and I_b/N_b), and the probability of virus transmission from
 267 the biting and infectious mosquito to the human (β_h),

$$268 \quad \lambda_h = \frac{B_g}{N_h} \beta_h \frac{I_g}{N_g} + \frac{B_b}{N_h} \beta_h \frac{I_b}{N_b} \quad (4)$$

269 The force of infection from humans to *Ae. aegypti* and to *Ae. albopictus* (λ_g and λ_b ,
 270 respectively) were the product of the number of bites per mosquito per day (B_g/N_g and B_b/N_b ,
 271 respectively), the probability that the bitten human was infectious (I_h/N_h), and the probability of
 272 pathogen transmission from an infected human to the biting mosquito (β_g and β_b , respectively).

$$273 \quad \lambda_g = \frac{B_g}{N_g} \beta_g \frac{I_h}{N_h} \quad (5)$$

$$274 \quad \lambda_b = \frac{B_b}{N_b} \beta_b \frac{I_h}{N_h} \quad (6)$$

275 **Model parameters**

276 The contact rates of humans and *Ae. aegypti* (B_g) or *Ae. albopictus* (B_b) were obtained
 277 from this study. Other parameters were obtained from other sources (Table 1).

278 **Table 1** Model parameters, their baseline values and ranges, and sources [20,27-34].

	Parameter	Unit	Value	Range	Source
H_0	Human population size, ORL	Human	10,157	-	US census 2016 estimates
	Human population size, TAM		7,385	-	
B_g	<i>Ae. aegypti</i> -human contact rate, ORL	Day ⁻¹	26,389	17,094 - 35,684	from this study
	<i>Ae. aegypti</i> -human contact rate, TAM		5,484	3,777 - 7,197	
B_b	<i>Ae. albopictus</i> -human contact rate, ORL		40,916	26,504 - 55,329	
	<i>Ae. albopictus</i> -human contact rate, TAM		9,834	6,773 - 12,895	
β_h	Probability of transmission from mosquito to human given an infectious bite	-	0.33	0.10 - 0.75	[20,27]
β_g	Vector competence for <i>Ae. aegypti</i>	-	0.25	0.03 - 0.76	[28,29]
β_b	Vector competence for <i>Ae. albopictus</i>	-	0.06	0.01 - 0.56	[28,29]
$1/v_g$	EIP for <i>Ae. aegypti</i>	Day	6.5	2 - 33	[30]
$1/v_b$	EIP for <i>Ae. albopictus</i>				
$1/v_h$	IIP	Day	6	3 - 10	[31]
Ψ_g	Per capita recruitment rate of <i>Ae. aegypti</i>	Day ⁻¹	4.93	3.89 - 5.97	[32]
Ψ_b	Per capita recruitment rate of <i>Ae. albopictus</i>				
K_g	Carrying capacity of <i>Ae. aegypti</i>	Mosquito	10 H_0	3 H_0 - 17 H_0	Estimated
K_b	Carrying capacity of <i>Ae. albopictus</i>				
$1/\gamma_h$	Viremic period in human	Day	5	4 - 14	[31,33]
$\mu_h = \Psi_h$	Per capita death and birth rate for human	Year ⁻¹	1/75.7	1/74.9 - 1/81.3	CDC's wonder database
μ_g	Per capita death rate for <i>Ae. aegypti</i>	Day ⁻¹	1/18	1/11 - 1/55	[32,34]
μ_b	Per capita death rate for <i>Ae. albopictus</i>				

279

280 The bite number, ρ_h , was the total number of bites a typical human received per person
 281 per day, regardless of mosquito species, and was estimated from our survey. The proportion of
 282 bites, p_v , that belonged to mosquito species v was estimated from HLC data. The number of

283 mosquito bites that belonged to mosquito species v that humans received per person per day (or
 284 the bite exposure rate) was

$$285 \quad \rho_{hv} = \rho_h \cdot p_v \quad (7)$$

286 If H_0 was the human population size, then, the number of mosquito bites from mosquito
 287 species v that all humans in the population received per day (or the contact rate) is

$$288 \quad B_v = \rho_{hv} \cdot H_0 \quad (8)$$

289 **The basic reproductive number (R_0)**

290 The calculations and model analyses were done in MATLAB R2018a (version 9.4.0).
 291 The model outcomes of interest were 1) the initial rate of disease spread by evaluating the basic
 292 reproduction number (R_0) and 2) the initial transient disease dynamics by evaluating the timing
 293 and magnitude of the first epidemic peak. Disease-free equilibrium points are steady-state
 294 solutions where there is no disease; i.e., no exposed or infectious individuals for both humans and
 295 mosquitoes. Let $X = (N_h, E_h, I_h, R_h, N_g, E_g, I_g, N_b, E_b, I_b)$, then the model for dengue transmission
 296 had exactly one disease-free equilibrium point, $X_{dfe} = (H_0, 0, 0, 0, K_g, 0, 0, K_b, 0, 0)$, with no
 297 disease in the population.

298 In a homogeneously mixed population, the basic reproduction number (R_0) is the
 299 expected number of secondary infections that one infectious individual would cause over the
 300 duration of the infectious period in a fully susceptible population [35]. From this definition, it can
 301 be logically interpreted that when $R_0 < 1$, each infectious individual produces less than one new
 302 infected individual on average and the pathogen transmission ‘dies out’ from the population.
 303 Conversely, if $R_0 > 1$, the pathogen is able to invade the susceptible population.

304 The next generation operator approach was used to calculate R_0 [36]. The description of
 305 the calculation of R_0 using the next generation operator is described in detail in Appendix A,
 306 which resulted in R_0 expression:

$$307 \quad R_0 = \sqrt{\frac{\beta_h B_g v_g}{K_g \mu_g (\mu_g + v_g)} \cdot \frac{\beta_g B_g v_h}{H_0 (\mu_h + v_h) (\mu_h + \gamma_h)} + \frac{\beta_h B_b v_b}{K_b \mu_b (\mu_b + v_b)} \cdot \frac{\beta_b B_b v_h}{H_0 (\mu_h + v_h) (\mu_h + \gamma_h)}} \quad (9)$$

308 In a fully susceptible human population, the number of new human infections caused by
 309 one infected *Ae. aegypti*, or the basic reproductive number for the disease transmission from *Ae.*
 310 *aegypti* to human, was

$$311 \quad R_{hg} = \beta_{hK_g} \frac{B_g v_g}{(\mu_g + v_g)\mu_g} \quad (10)$$

312 In this expression, $\frac{v_g}{\mu_g + v_g}$ was the probability of *Ae. aegypti* surviving the exposed stage
 313 and becoming infectious. $\frac{1}{\mu_g}$ was the lifespan of *Ae. aegypti*. The product of these two terms, or
 314 $\frac{v_g}{(\mu_g + v_g)\mu_g}$, equaled to the average number of days that *Ae. aegypti* was infectious. As a result, R_{hg}
 315 can be seen as the product of 1) the number of bites per day per mosquito, or $\frac{B_g}{K_g}$, 2) the probability
 316 of a successful transmission per bite, or β_h , and 3) the number of days in the infectious period, or
 317 $\frac{v_g}{(\mu_g + v_g)\mu_g}$.

318 Similarly, the basic reproductive number for the disease transmission from *Ae. albopictus*
 319 to human, from human to *Ae. aegypti*, and from human to *Ae. albopictus*, respectively, was

$$320 \quad R_{hb} = \beta_{hK_b} \frac{B_b v_b}{(\mu_b + v_b)\mu_b}, \quad (11)$$

$$321 \quad R_{gh} = \beta_{gH_0} \frac{B_g v_h}{(\mu_h + v_h)(\mu_h + \gamma_h)}, \quad (12)$$

322 and

$$323 \quad R_{bh} = \beta_{bH_0} \frac{B_b v_h}{(\mu_h + v_h)(\mu_h + \gamma_h)}. \quad (13)$$

324 The basic reproduction number R_0 in (9) can be expressed in terms of these quantities as

$$325 \quad R_0 = \sqrt{R_{hg}R_{gh} + R_{hb}R_{bh}} \quad (14)$$

326 For vector-borne viral transmission between two humans, two stages of the transmission
 327 process are involved: the transmission from human “A” to mosquito “B” (generation 1), and then
 328 from mosquito “B” to another human “C” (generation 2). The number of mosquitoes “B” caused
 329 by an infectious human “A” is R_{bh} (or R_{gh}), and the number of humans “C” caused by each

330 infectious mosquito “B” is R_{hb} (or R_{hg}). After two generations, the total number of secondary
331 human-to-human cases for both mosquito species is $R_{hg}R_{gh} + R_{hb}R_{bh}$. Therefore, the basic
332 reproductive number (R_0), which characterizes the number of cases in one generation, is the
333 geometric average of the cases in two generations, that is $\sqrt{R_{hg}R_{gh} + R_{hb}R_{bh}}$.

334 **Sensitivity analysis**

335 Because the transmission parameters are only known approximately, it is important to
336 understand how variations in these parameters affect model outcomes. To quantify the impact of
337 changes in parameters on R_0 , three types of sensitivity analysis were performed: a local
338 sensitivity analysis, an extended sensitivity analysis, and a global sensitivity analysis.

339 In the local sensitivity analysis, sensitivity indices were derived to quantify how small
340 changes in the parameter of interest p caused variability in the model output of interest q . If an
341 input parameter p changed by $x\%$, then the output quantity q changed by $S_p^q \cdot x\%$. As such, the
342 sensitivity index’s magnitude determines the relative importance of the model parameters on the
343 model predictions. The sign of the sensitivity index indicates the direction of change of the output
344 in response to the parameter change. The sensitivity indices of R_0 were analytically computed by
345 evaluating partial derivatives of R_0 (Eq. 9) with respect to each parameter of interest at the
346 baseline value, multiplied by a scaling factor ($S_p^q = \frac{\partial q}{\partial p} \cdot \frac{p}{q}$). As a result, the local sensitivity indices
347 are valid only at a small range around the parameter baseline values.

348 In the extended sensitivity analysis, the responses of R_0 to the variations in each
349 parameter of interest are calculated over the entire possible range of that parameter (Table 1),
350 while fixing all other parameters at their baseline. The extended local sensitivity analysis curves
351 were plotted to depict the derivative of R_0 as a function of the model parameter of interest at all
352 values within its possible range.

353 In the global sensitivity quantification, the values of R_0 were calculated using multiple
354 combinations over the full range of all the parameters. The parameters were treated as random

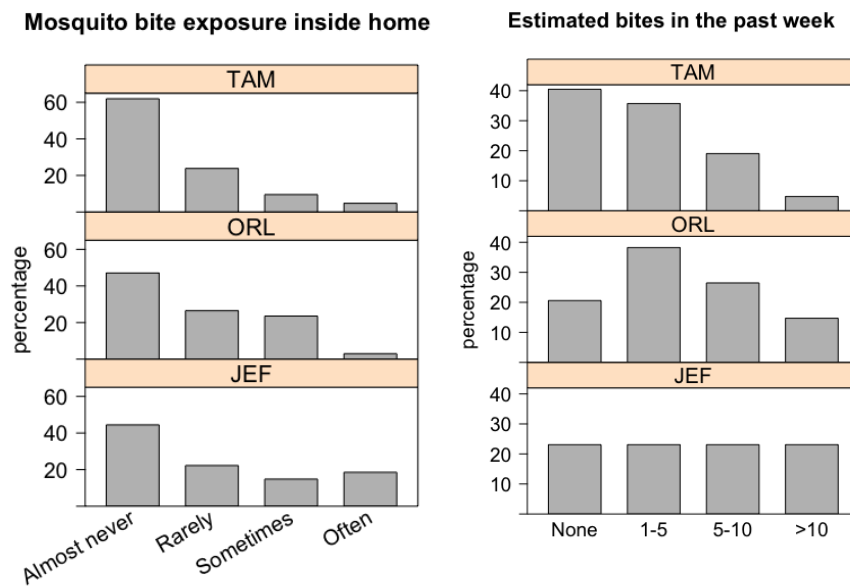
355 variables (all parameters can simultaneously take any values within their possible ranges), and R_0
356 had a distribution, which depended on the distributions of parameters. In this analysis, each of the
357 model parameters was assumed to vary independently from each other and has a uniform
358 distribution. The description of sensitivity analyses was given in more detail in the previous
359 publication [20]. All sensitivity analyses were done in MATLAB R2018a (version 9.4.0).

360 Results

361 Exploratory survey of mosquito bite exposure in adults in the Greater New Orleans

362 Region

363 In the preliminary survey, the total number of retrieved questionnaires was 104 (ORL,
364 33; JEF, 24; TAM, 47). The average return rate across study sites was 20.7%. The results are
365 shown in Fig 1



366

367 **Fig 1.** Results from the preliminary survey showing the frequency of bite exposure inside homes and the
368 estimated numbers of bites research participants experienced in the past 7 days. The percentages of
369 participants choosing each answer of the multiple-choices questions are shown.

370 The preliminary results suggested variations between study sites. Research participants in
371 JEF reported higher exposure to mosquito bites than research participants in ORL and TAM. In

372 TAM, around 40% of research participants indicated that they did not receive any mosquito bites
373 in the past 7 days. While in ORL, 38% of research participants chose “1-5” bites in the past 7
374 days. In JEF, equal proportions (23%) of research participants reported being bitten more than 10
375 times, 5-10 times, 1-5 times, and none in the past 7 days.

376 When asked how often they experienced mosquito bites inside of their homes, 19% of
377 research participants from JEF chose “often” as the answer, higher than the other two study sites
378 (both were <5%). In all study sites, the place where people most often experienced outdoor
379 mosquito bites was around their homes (78%, 72%, 56% for TAM, JEF, and ORL, respectively).
380 In ORL, “public space” was also reported as a place where people most often experienced
381 mosquito bites (32%).

382

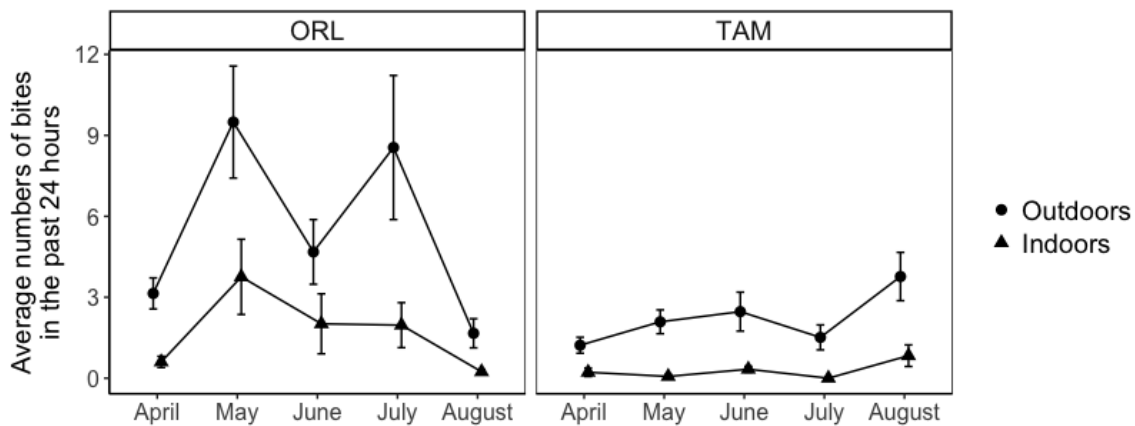
383 **Mosquito bite exposure rates in adults in the Greater New Orleans Region**

384 For the second survey, a total of 941 and 801 questionnaires were distributed in ORL and
385 TAM, respectively. The average numbers of addresses per block were 23.53 (SD = 7.90) for ORL
386 and 20.03 (SD = 3.44) for TAM. In ORL, a total of 91 questionnaires were retrieved, with an
387 average return rate of 10.06% (SD = 6.46%) per block. In TAM, a total of 94 questionnaires were
388 retrieved, with an average return rate of 11.35% (SD = 8.26%) per block.

389 The average numbers of adults (>18 years old) per household were 1.84 for ORL (SD =
390 0.73) and 2.11 for TAM (SD = 0.62). Graphs showing the gender and age distribution of research
391 participants in both study sites are shown in Supplementary Figure 2. In total, research
392 participants included 90 females, 70 males, and 25 individuals who did not indicate their gender.
393 Of these, one person was between 18-25 years old, 38 were between 26-40 years old, 78 were
394 between 41-65 years old, 63 were more than 65 years old, and 5 failed to indicate their age range.

395 Overall, the reported numbers of mosquito bites that occurred outdoors and indoors
396 within the past 24 hours in ORL, after adjustment with sampling weights, were 5.48 (SE=0.90)

397 and 1.68 (SE=0.46), respectively. The reported numbers of bites that occurred outdoors and
398 indoors within the past 24 hours in TAM, after adjustment with sampling weights, were 2.28
399 (SE=0.34) and 0.32 (SE= 0.13), respectively. In both study sites, the average numbers of reported
400 bites that occurred outdoors were significantly higher than indoors (Wilcoxon rank sum test,
401 ORL: $df = 34$, p -value <0.001 , TAM: $df = 30$, p -value <0.001). In addition, the reported numbers
402 of bites were significantly higher in ORL compared to TAM for both outdoor and indoor settings
403 (Wilcoxon Rank Sum test, outdoors: $df = 66$, p -value= 0.003; indoors: $df = 66$, p -value <0.001).
404 The average reported numbers of bites that occurred outdoors and indoors, after adjustment with
405 sampling weights, within the past 24 hours in both study sites across months are shown in Fig 2.



406

407 **Fig 2** The average numbers of mosquito bites per person, after adjustment with sampling weights, in the past 24 hours
408 that research participants reported are shown by sites and month of data collection. The circles represent the outdoor
409 bites and the triangles represent indoor bites. Error bars represent the standard errors.

410 **Factors affecting bite exposure in adults in the Greater New Orleans Region**

411 For research participants who reported receiving outdoor mosquito bites within the past
412 24 hours, they were asked to indicate the locations that they experienced these bites. In TAM, 47
413 participants or around 90% reported being bitten around their homes (answers such as ‘front
414 yard’, ‘backyard’, ‘on dock’, ‘sitting in my open garage’), whereas 5 participants or around 10%
415 reported being bitten both around their homes *and* at public spaces (answers such as ‘backyard
416 and dog park’ and ‘yard and during a walk’). In ORL, 33 participants or around 59% reported

417 being bitten around their homes (answers such as ‘backyard’, ‘front porch’, and ‘side yard’), 6
418 participants or 11% reported being bitten at public spaces (answers such as ‘outside while at
419 work’, ‘while walking the dog’, and ‘walking along Crescent City park and inside of an
420 indoor/outdoor bar’), and 17 participants or 30% reported being bitten both around their homes
421 *and* at public spaces (answers such as ‘backyard, while out walking’ and ‘Clouet garden and my
422 backyard’).

423 Information about the time spent outdoors within the past 24 hours was collected from
424 research participants (Supplementary Figure 3). After adjustment with sampling weights, research
425 participants in ORL spent 41.78 minutes (SE = 7.43) and 67.47 minutes (SE = 6.91) outdoor
426 during the weekday and weekend on average, respectively. After adjustment with sampling
427 weights, research participants in TAM spent 54.33 minutes (SE = 5.53) and 51.00 minutes (SE =
428 8.17) outside during the weekday and weekend on average, respectively. The difference of the
429 time spent outside between the weekend and weekday was significant for research participants in
430 ORL (Wilcoxon Rank Sum test, $df = 34$, p -value = 0.02) but not for research participants in TAM
431 (Wilcoxon Rank Sum test, $df = 30$, p -value = 0.3). In addition, the difference of the time spent
432 outside between research participants in ORL and TAM was statistically significant for the
433 weekend (Wilcoxon Rank Sum test, $df = 32$, p -value = 0.02) but not during the weekday
434 (Wilcoxon Rank Sum test, $df = 32$, p -value = 0.3).

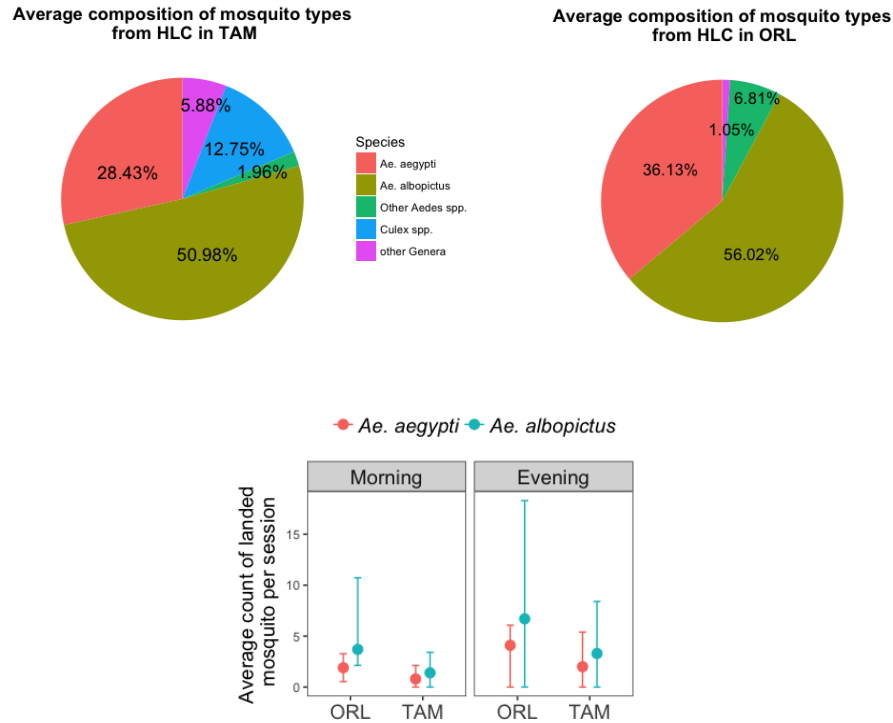
435 The time spent outside during the time period between 5 pm to 8 pm (or evening time),
436 and 8 pm to 6 am (or nighttime) showed significant correlations with reported bite numbers using
437 Spearman’s correlation test. The correlation coefficient was 0.25 (p -value = 0.003) and 0.28 (p -
438 value <0.001) for the evening and nighttime, respectively. The time spent outside during the time
439 period between 6 am to 10 am (or morning time), and 10 am to 5 pm (or daytime) did not show
440 significant correlations with reported bite numbers (Spearman’s correlation test; p -value = 0.078
441 and 0.975, respectively).

442 A generalized linear model analysis was used to determine which variables are associated
443 with how much time the research participants reported spending outside in the evenings and at
444 night. A table showing the model's result is shown in Supplementary Table 2. Only the age range
445 of research participants and the weekend/weekday setting showed significant associations with
446 the time participants reported spending outside in the evening and night. Specifically, older
447 participants spent less time outside in the evening and night than younger participants. Research
448 participants also spent less time outside on weekdays than on weekends.

449 Another generalized linear model analysis was used to determine the effect of study site,
450 the month of data collection, total time spent outside in the evening and night, and gender of
451 research participants on the reported numbers of outdoor bites. The results, detailed in
452 Supplementary Table 3, indicated that the time spent outside in the evening and night, the month
453 of data collection (May, July, and August), and study site show significant associations with the
454 reported outdoor bite numbers. The results show that, when controlled for other variables
455 including the time they spent outside, research participants in ORL reported experiencing higher
456 mosquito bites than participants from TAM. Gender did not show a significant association with
457 the reported bite numbers (p-value = 0.053).

458 **Determining mosquito species contributing to bite exposure in the Greater New** 459 **Orleans using Human Landing Capture.**

460 The average composition of female mosquito species and types captured during HLC in
461 both study sites are shown in the top graphs of Fig 3. In ORL, on average 56.02% of landed
462 female mosquitoes were *Ae. albopictus* and 36.13% were *Ae. aegypti*. In TAM, on average
463 50.98% of landed mosquitoes were *Ae. albopictus* and 28.43% were *Ae. aegypti*. In ORL, species
464 other than *Ae. aegypti* and *Ae. albopictus* that were captured included: *Ae. taeniorhynchus*, *Ae.*
465 *vexans*, *Mansonia titillans* and *Ae. infirmatus*. In TAM, other species included: *An. bradleyi*, *Cx.*
466 *salinarius*, *Cx. restuans*, *Ae. taeniorhynchus*, and *Ae. sollicitans*.



467

468

469 **Fig 3.** Top: pie graphs showing the average composition of mosquito types captured during HLC in TAM and ORL.

470 Bottom: average numbers of landed female *Ae. aegypti* and *Ae. albopictus* in ORL and TAM during the 1.5 hour of

471 HLC sessions in the morning and evening.

472 The average numbers of female *Ae. aegypti* and *Ae. albopictus* landed during 40 HLC
473 sessions are shown in the bottom graph of Fig 3. In ORL, the average numbers of landed female
474 *Ae. aegypti* in the morning and evening HLC session (1.5 hour) were 1.9 (SD = 1.37) and 4.1 (SD
475 = 1.97), respectively. The average numbers of landed female *Ae. albopictus* in the morning and
476 evening HLC session were 3.7 (SD = 7.03) and 6.7 (SD = 11.60), respectively. In TAM, the
477 average numbers of landed female *Ae. aegypti* in the morning and evening HLC session were 0.8
478 (SD = 1.32) and 2.0 (SD = 3.40), respectively. The average numbers of landed female *Ae.*
479 *albopictus* in the morning and evening HLC session were 1.4 (SD = 2.01) and 3.3 (SD = 5.10),
480 respectively. Averaging data from both study sites, the number of landed mosquitoes was higher
481 in the evening than in the morning for both *Aedes* species. However, the difference is statistically
482 significant only for *Ae. aegypti* and not for *Ae. albopictus* (Wilcoxon Rank Sum test, p-value =

483 0.04 and 0.08, respectively). In addition, averaging data from both morning and evening sessions,
 484 the number of landed mosquitoes in ORL was significantly higher than in TAM for *Ae. aegypti*
 485 but not for *Ae. albopictus* (Wilcoxon Rank Sum test, p-value = 0.002 and 0.2, respectively).

486 **Basic Reproductive Number (R_0) and the initial transmission of DENV**

487 The model analysis simulated a situation where one infectious human was introduced into
 488 fully susceptible populations of humans and mosquitoes. Table 2 shows the result from the model
 489 analysis using different values of local human-mosquito contact rates, calculated using equation
 490 (7) and (8), while holding other parameters at baseline values. The output of interest includes R_0 ,
 491 the percentage of infected and recovered human at their peaks, and the numbers of days before
 492 the number of infected and recovered human reach their peaks.

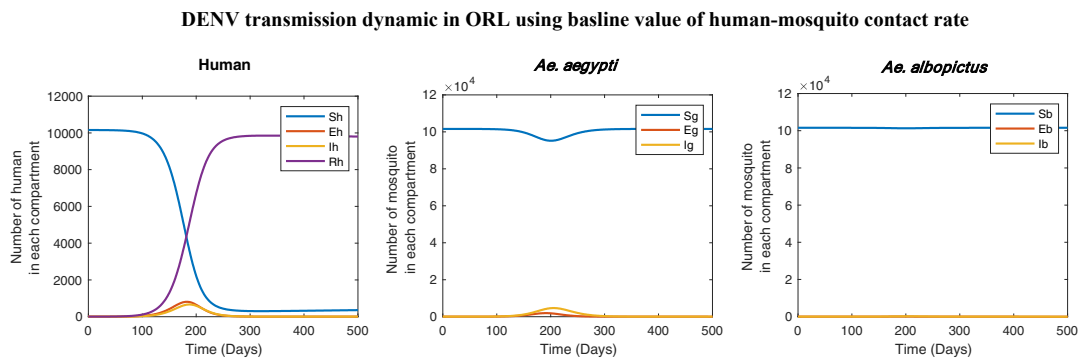
493 **Table 2** Results from the model analysis using different values of local human-mosquito contact rates.

Parameter	R_0	Infected human at its peak		Recovered human at its peak	
		Percentage over total population	Time at the peak (day)	Percentage over total population	Time at the peak (day)
Using human-mosquito contact rates from ORL					
baseline values	2.41	6.53%	188	97.00%	332
minimum values	1.56	1.30%	510	64.70%	907
maximum values	3.26	10.83%	124	99.67%	213
Using human-mosquito contact rates from TAM					
baseline values	0.73	-	-	-	-
minimum values	0.50	-	-	-	-
maximum values	0.96	-	-	-	-

494
 495 Given values of human-mosquito contact rates acquired from both study sites, only the R_0
 496 during the initial DENV transmission in ORL exceed 1. When using the baseline value of human-
 497 mosquito contact rate from ORL, the calculated R_0 for DENV transmission in the area was 2.41
 498 and the infected human number peaked at day 188th after the virus introduction. When using the
 499 minimum value for the contact rate from ORL, R_0 was greater than 1 even though the outbreak
 500 was less explosive. The infected human number peaked at day 510th after the initial virus
 501 introduction. R_0 value was highest (3.26) for the maximum value of the contact rate from ORL,

502 and the number of infected humans peaked at day 124th. However, none of the human-mosquito
503 contact rate values quantified in TAM resulted in an R_0 exceeding 1, and therefore a small initial
504 infection would die out.

505 Given the baseline value of human-mosquito contact rate in ORL, the number of infected
506 *Ae. aegypti* at its peak was 4,647. This is higher than infected *Ae. albopictus*, where their number
507 at the peak was 182 (Fig 4). When using the maximum value of human-mosquito contact rate in
508 ORL, the number of infected *Ae. aegypti* and *Ae. albopictus* at their peaks were 8,779 and 360,
509 respectively. Finally, when using the minimum value of human-mosquito contact rate in ORL, the
510 number of infected *Ae. aegypti* and *Ae. albopictus* at their peaks were 713 and 27, respectively.



512 **Fig 4** Model analysis of DENV transmission in ORL using baseline value of human-mosquito contact rate.

513 **Local sensitivity analysis**

514 The local sensitivity indices of R_0 with respect to model parameters are shown in Table 3.
515 For both transmission scenarios in ORL and TAM, the R_0 is most sensitive to 1) *Ae. aegypti*-
516 human contact rate (B_g), 2) the probability of DENV transmission from mosquito to human given
517 an infectious bite (β_h), and 3) the recovery rate of human (or the inverse of viremic period; γ_h),
518 evaluated at their baseline values. At the baseline values, the basic reproductive number is least
519 sensitive to the inverse of the intrinsic incubation period (v_h) and human death rate (μ_h).

520

521 **Table 3.** Sensitivity indices of R_0 with respect to model parameters at the baseline values.

Parameter	ORL ($R_0 = 2.41$)	TAM ($R_0 = 0.73$)
B_g	0.6341	0.5644
β_h	0.5000	0.5000
γ_h	-0.4999	-0.4999
μ_g	-0.4012	-0.3571
B_b	0.3659	0.4356
K_g	-0.3171	-0.2822
β_g	0.3171	0.2822
μ_b	-0.2315	-0.2756
K_b	-0.1829	-0.2178
β_b	0.1829	0.2178
v_g	0.0841	0.0749
v_b	0.0485	0.0578
μ_h	-0.0002	-0.0002
v_h	0.0001	0.0001

522

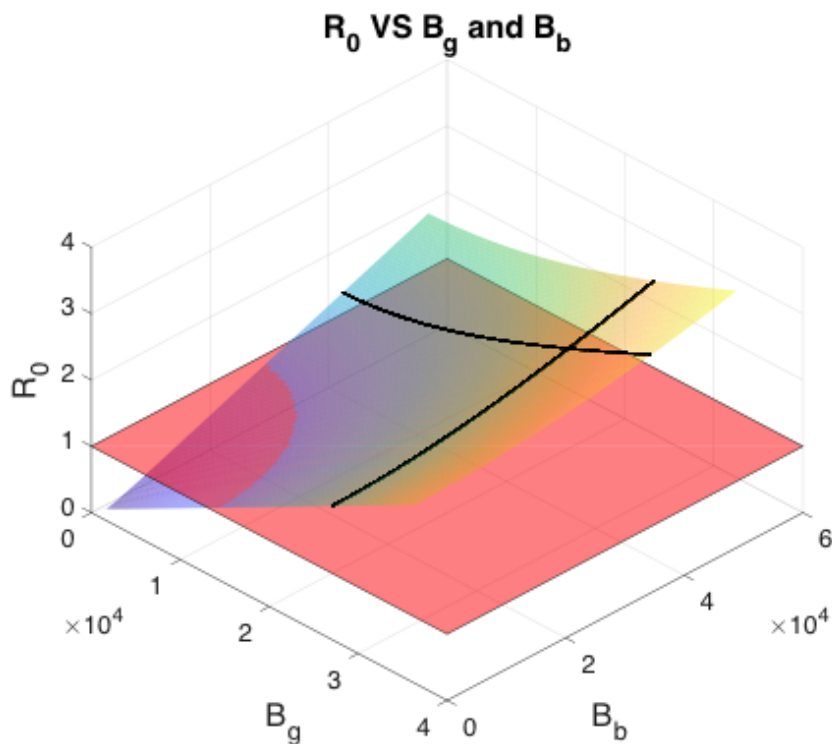
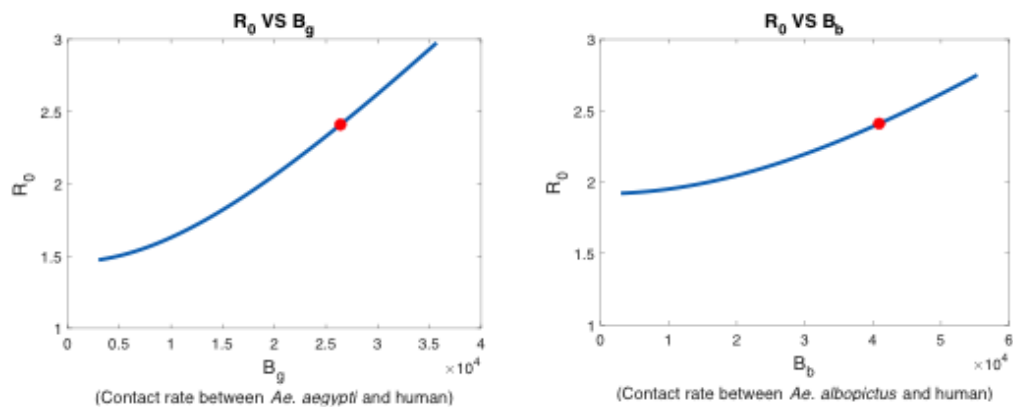
523 The sign of the sensitivity index indicates the relationship between the direction of
524 changes in R_0 and model parameters. For example, the sensitivity indices of R_0 with respect to
525 human-mosquito contact rates (both B_g and B_b), evaluated at their baseline values, are positive.
526 Therefore, as the contact rate between mosquito and human increases, the R_0 also increases. On
527 the contrary, the sensitivity indices of R_0 with respect to γ_h , evaluated at their baseline values, are
528 negative. As a result, as the human recovery rate increases (i.e. viremic period decreases), the R_0
529 decreases. Another observation is the negative value of the sensitivity indices of R_0 with respect
530 to the mosquito carrying capacity (both K_g and K_b), evaluated at their baseline values. This can be
531 interpreted that as the mosquito carrying capacity increases, the R_0 decreases. The mathematical
532 explanation for this unexpected relationship is discussed in the Discussion section.

533 The relative ranking of the parameter importance was almost the same between the two
534 scenarios (Table 3). The only exception is that B_b , or *Ae. albopictus*-human contact rate, becomes
535 relatively less important at determining R_0 in the ORL scenario compared to TAM. This results

536 from the assumption that *Ae. Albopictus* has a lower vector competence than *Ae. aegypti*, and *Ae.*
537 *aegypti*-human has a higher contact rate in the ORL.

538 Extended sensitivity analysis

539 The extended sensitivity analysis plots of R_0 with respect to the mosquito-human contact
540 rate for the transmission scenario in ORL are shown in Figure 6. The extended sensitivity analysis
541 plots of R_0 to other selected model parameters for ORL and TAM are shown in Supplementary
542 Figure 4 and 5, respectively.



543

544 **Fig 5** The extended sensitivity analysis plots of R_0 with respect to the human-mosquito contact rate for the
545 model analysis of DENV transmission in ORL. In the top graphs, the red dots represent the R_0 at the
546 contact rate baseline values. In the bottom graph, the red plane represents where $R_0 = 1$ and the black lines
547 represent the R_0 values at baseline contact rates of each of the two *Aedes* species and humans. The point
548 where the two lines meet represents the R_0 value at the baseline contact rates of both *Aedes* species and
549 humans.

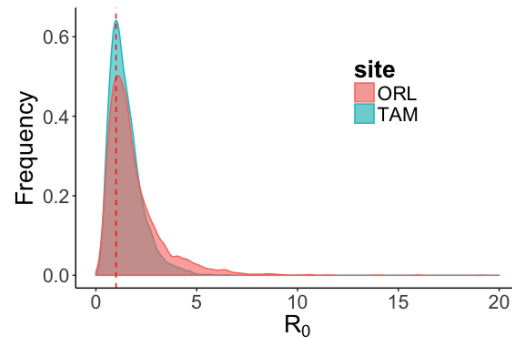
550 First, consider the top two graphs of Fig 5, which show how the R_0 value changes in
551 response to changes in the *Ae. aegypti*-human contact rate (B_g ; top left panel) and the *Ae.*
552 *albopictus*-human contact rate (B_b ; top right panel), while holding all other parameters at their
553 baseline values. Both plots show curves with positive trends, indicating that a decrease in contact
554 rate, while holding other parameters at their baselines, will cause R_0 to decrease. However, this
555 relationship is not linear; as the contact rate decreases, the slope becomes smaller. That is, the
556 reduction in human-mosquito contact rate, when focused on only one vector species at a time,
557 becomes less effective at reducing R_0 when the contact rate is already small. In fact, in the ORL
558 scenario, reducing the contact rate between humans and only one vector species at a time will fail
559 to reduce R_0 below 1. This is because the contact rate between humans and the other vector
560 species is high enough to maintain the transmission.

561 Next, consider the bottom graph in Fig 5, which shows how R_0 changes in response to the
562 changes in both B_g and B_b simultaneously, while holding other parameters at their baseline
563 values. In this case, the reduction of both B_g and B_b at the same time below certain threshold
564 values will result in $R_0 < 1$.

565 **Global sensitivity analysis**

566 Figure 7 shows the distribution of R_0 calculated from combinations of model parameter
567 values, which were sampled uniformly and independently within their possible ranges. The R_0
568 distribution for the ORL scenario was wider at the base and had a longer tailed distribution,
569 indicating that there was a higher variation in the outcomes. The percentage of scenarios (or the

570 combinations of parameter values) that resulted in an $R_0 > 1$ indicated how likely DENV was to
571 spread in either location. In the ORL case, 74.52% of scenarios resulted in an $R_0 > 1$. In TAM,
572 68.80% of scenarios resulted in an $R_0 > 1$. As such, ORL was more receptive to an initial outbreak
573 of DENV than TAM.
574



575
576 **Figure 7.** The frequency distribution of R_0 values calculated from combinations of model parameter values
577 sampling uniformly and independently. The vertical dashed line at $R_0=1$ indicates the threshold value for an
578 outbreak.

579

580 Discussion

581 Mosquito bite exposure was investigated using a questionnaire survey to ask research
582 participants about their past experience receiving mosquito bites. We found that the mosquito bite
583 exposure on research participants occurred more frequently in the outdoors than indoors in both
584 study sites. The location that research participants most often reported being exposed to mosquito
585 bites was around their homes. We quantified the correlation between the reported bite number
586 and the time spent outside in the evenings and at night. After controlling for the time duration
587 spent outside, there was a significant effect of study site on the outdoor biting rate, where
588 participants in ORL reported receiving more mosquito bites than participants in TAM. In places
589 such as the Greater New Orleans Region where the mosquito bite exposure between indoors and

590 outdoors may be different, the human-mosquito contact rate depends on the density of host-
591 seeking female mosquitoes and human behavior, such as the time spent outside.

592 Interestingly, the indoor bite exposure rate was also higher for ORL than in TAM. The
593 potential reason for this difference was not investigated in this study. According to the 2016 ACS
594 5-year estimates, the median household income in TAM is 42% higher than in ORL
595 (Supplementary Table 1). It is possible that factors such as the integrity of the wall, the
596 availability of air conditioners, combined with human behaviors (keeping doors or windows
597 open) determine the difference in indoor bite exposure rate [37]. Future study is needed to
598 investigate the relative importance of these factors on indoor mosquito bite exposure.

599 Only a few other studies have used surveys to investigate mosquito bite exposure. A
600 study by Dowling *et al.* asked research participants in suburbs of Washington DC how often they
601 were bitten by mosquitoes. Out of 246 participants, 48% chose ‘Everyday’, 28% chose ‘Few days
602 a week’, and 24% chose ‘Few days a month or fewer’ [38]. A similar study by Halasa *et al.*
603 interviewed residents in two counties of New Jersey and found that during a typical summer
604 week, 80.2% of respondents reported being bitten at least once and 77.7% were bitten while
605 outdoors [39]. In Halasa’s study, bite exposure occurred most often in the evening (52.1%),
606 followed by at night (31.4%), and late afternoon (30.6%). A study by Read *et al.* used a unique
607 study design to compare the number of mosquito bites that participants thought they received
608 while sitting outside for 5 minutes with the number of mosquitoes captured concurrently on a
609 staff person using a Whole Person Bag Sampler [40]. The study showed that respondents’
610 reported bites received during the 5-min blinded test time increased with increasing trap count.
611 However, there was a higher discrepancy between the reported bites and the trap count at the
612 lower trap count.

613 The HLC data from this study indicated that there were higher numbers of host-seeking
614 mosquitoes in ORL than in TAM, and more in the evening than in the morning. Even though this
615 study was not designed to compare the bite survey to HLC, the observations from both methods

616 were congruous. For example, the higher reported mosquito bite exposure in ORL mirrored the
617 higher number of host-seeking mosquitoes in that site, compared to TAM. In addition, the
618 correlation between the reported outdoors time and the amount of mosquito bites was found only
619 in the evening and nighttime, but not in the morning. This finding was consistent with our HLC
620 data and other studies, which found higher numbers of host-seeking *Ae. aegypti* in the evenings
621 than in the mornings [24,41]. Future study is needed to investigate the correlation between the
622 reported bite exposure level from surveys and the number of landed mosquitoes from HLC
623 experiments.

624 Our model analysis showed that the human-mosquito contact rate played an important
625 role in determining contrasting outcomes in dengue transmission simulated in the two study sites.
626 The local sensitivity indices indicated that the contact rate between humans and *Ae. aegypti* was
627 the most important parameter determining the R_0 , and was more important than the contact rate
628 between humans and *Ae. albopictus*. This was because of the difference in the vector competence
629 between the two species. *Ae. aegypti* is thought to be a more competent vector [42] and we set its
630 vector competence value to be higher. Our laboratory experiment to test vector competence of the
631 locally collected mosquitoes also suggested that the local *Ae. aegypti* was more competent than
632 the local *Ae. albopictus* (data not shown).

633 Interestingly, changes in the carrying capacity of mosquitoes (which controlled their
634 population size) showed an inverse relationship with the changes in R_0 , while holding other
635 parameters at their baselines. That is, as the mosquito population size decreases, then the potential
636 for disease outbreak increases. This is counter-intuitive because one may expect the risk of an
637 outbreak to be smaller when the vector density is low. However, the assumption of this model is
638 that the contact rate is frequency-dependent: it does *not* depend on human or mosquito density.

639 This assumption may be valid when human, and mosquito variables contribute to a fixed
640 amount of bites that is compromised by both the mosquito's desire to blood-feed and the number
641 of bites humans can tolerate. Under this assumption, the biting rate *per mosquito* (B_g/K_g and

642 B_b/K_b) would increase as the carrying capacity (K_g and K_b) of mosquitoes decreases. The increase
643 in this biting rate *per mosquito* results in a higher outbreak potential. Even though this
644 explanation is justifiable mathematically, the real-world mechanisms will likely be more
645 complicated, and may result in a different transmission outcome. Nonetheless, when designing a
646 mosquito-borne disease control program, especially in endemic areas, control tools that reduce
647 contact between human and mosquito should be implemented along with those that reduce
648 mosquito density.

649 Mathematical models are a simplified simulation of a real world complex process. As
650 such, the models are biased and limited by their assumptions and parameter values. In our model,
651 we assumed uniform distributions of human and mosquito density in both space and time. In
652 reality, this is unlikely to hold true. For example, the mosquito population size in the Southern US
653 fluctuates significantly as a response to seasons. When the simulated time period spans across
654 several seasons, then the model parameters need to account for the fluctuating mosquito's
655 carrying capacity and death rate.

656 In addition, a deterministic model was utilized. Even though this model type has been
657 applied in many disease systems due to its simplicity and clarity [43,44], it ignores heterogeneity
658 and stochasticity inherent in natural disease transmission. Early in the disease invasion stage,
659 when there are only a few infectious hosts, stochasticity and chance events often play an
660 important role in determining the transmission course [45]. For example, infectious hosts can all
661 heal or die due to chance alone before transmission can take off even when R_0 is above one.

662 We also assumed that the contacts were evenly distributed among individuals. This
663 assumption rarely applies in the real world. Often, only a small fraction of individuals, known as
664 super-spreaders, contribute significantly to contacts and transmission events [46]. Studies have
665 shown that mosquito biting and bite exposure are associated with many variables such as human
666 body size, alcohol consumption, skin odor, housing type, or proximity to mosquito habitats [47].
667 In addition, behavioral changes that may be associated with more severe human cases (e.g. house-

668 ridden individuals) could result in differential bite exposure rates. Questionnaire-based surveys
669 may be a valuable tool that could be feasibly used to investigate how these factors impact
670 heterogeneity in mosquito bite exposure among individuals.

671 Another important factor determining the accuracy of the model's predictions is the
672 accuracy of the parameters' values. Human-mosquito contact rate has rarely been characterized in
673 the field and is among the least known parameters in mosquito-borne disease transmission. HLC
674 has been the traditional gold standard method, but its use is often impractical [48] and does not
675 take into account human lifestyles or other innate human variables. Molecular approaches to
676 profile the mosquito blood meal are expensive, time-consuming, and can only provide biting
677 patterns [49-51] and not rates (but see [52]). The use of questionnaire-based surveys, especially in
678 the form of door-hanger questionnaires, provides a low-cost, fast, and feasible alternative.

679 Despite their benefits, using surveys to approximate human-mosquito contact rates may
680 result in some biases. For example, in an attempt to get a full blood meal, a mosquito may probe
681 repeatedly on a host [53]. As a result, a person may report being bitten multiple times but the
682 contacts were with only one mosquito. In additions, the bites research participants received could
683 be from arthropods other than mosquitoes. Even though the participants were asked to indicate
684 the number of mosquito bites within the past 24 hours (instead of the past 7 days, as was done in
685 the preliminary survey), it is likely that there was a recall bias. To reduce this bias, a prospective
686 cohort study design could be used in future studies. In addition, only a small portion (~10%) of
687 the targeted population participated in the study. This may cause selection bias because the
688 decision to participate in the study may reflect inherent characteristics of the participants.
689 Subjects who decided to take part in a survey may have a strong interest or awareness in the study
690 topic [54]. By using other sampling methods or increasing sample size, selection bias could be
691 reduced.

692 Another limitation in our study results from the use of a small-scaled HLC to characterize
693 the mosquito compositions only at crepuscular periods. The composition of mosquitoes that may

694 contribute to bites during nighttime was not characterized. We expected that nighttime biters such
695 as *Culex* spp. and *Anopheles* spp. may contribute considerably to bites during this period.

696 Computational uncertainties are unavoidable in predicting the dynamics of an epidemic.
697 The baseline model parameters in Table 1, together with the human-mosquito contact rates
698 obtained through the survey, are only our best-guess estimates of the model parameters. Such
699 uncertainties in the parameters could affect the reliability of the model predictions. It is important
700 to emphasize that the quantitative values of the model outputs, such as R_0 , should not be taken at
701 face value. They only give us insight into potential outcomes of disease spreads. Fortunately, the
702 qualitative aspects of the model, such as the relative importance of the different factors are
703 usually robust and less sensitive to these assumptions.

704 The probability of a disease emergence in a new geographical area encompasses two
705 qualitative attributes: vulnerability and receptivity [55]. Vulnerability indicates the influx of
706 infected individuals into an area of interest, while receptivity reflects the local conditions that are
707 conducive for disease transmission. In this study, the risk of DENV outbreak was investigated
708 only at the level of receptivity. In Louisiana, a total of 45 imported cases were reported from
709 1980 to 2015 (Dengue Annual Report, Louisiana Office of Public Health, 2015). In general,
710 despite the highly receptive condition, the probability of a DENV outbreak could be lower due to
711 its low vulnerability.

712 In conclusion, we found that the use of a questionnaire-based survey is a feasible method
713 to estimate human-mosquito contact rates. It can be used to compare mosquito bite exposure
714 levels between settings in order to evaluate how environmental factors and intervention strategies
715 may impact disease risk. Most importantly, it may provide an avenue to investigate how changes
716 in human characteristics such as behaviors, lifestyles, use of clothing and personal protection, and
717 other innate variables affect mosquito bite exposure and the risk of infection in a way that is very
718 difficult to do with HLC. This information is indispensable if we want to predict how the
719 changing environment due to unplanned urbanization, poverty, and climate change impacts

720 mosquito-borne disease transmission. In addition, the use of mathematical models to simulate
721 disease transmission produces valuable information that helps us understand how changes in the
722 transmission variables may impact disease transmission. This type of knowledge facilitates the
723 planning of cost-effective disease prevention programs to target the most important transmission
724 factor which may lead to the largest reduction in transmission risk.

725

726 **Author contribution**

727 PT participated in conceptualization and study design, conducted field research, curated
728 data, participated in mathematical model development, and performed formal analysis and data
729 visualization. ZQ participated in model development and analysis, and participated in data
730 visualization. JOY participated in study design and data analysis, and validated mathematical and
731 statistical analyses. JMH participated in mathematical model development, and validated
732 mathematical model analyses. DMW participated in conceptualization and study design, oversaw
733 and coordinated the investigation, provided resources and mentorship for fieldwork execution and
734 data analysis. PT wrote the original draft. All authors read, edited, gave input, and approved the
735 final manuscript.

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741 **Appendix A**

742 Let $x = (E_h, I_h, E_g, I_g, E_b, I_b)^T$ and $dx/dt = F(x) - V(x)$, where $F(x)$ represents the rate of
 743 new infections entering the population, and $V(x) = V^-(x) - V^+(x)$ represents the rate of movement
 744 by other means out of, and into each compartment, respectively.

$$745 \quad \frac{dx}{dt} = \frac{d}{dt} \begin{bmatrix} E_h \\ I_h \\ E_g \\ I_g \\ E_b \\ I_b \end{bmatrix} = \begin{bmatrix} \lambda_h S_h \\ 0 \\ \lambda_g S_g \\ 0 \\ \lambda_b S_b \\ 0 \end{bmatrix} - \begin{bmatrix} (v_h + \mu_h)E_h \\ -v_h E_h + (\gamma_h + \mu_h)I_h \\ (v_g + \mu_g)E_g \\ -v_g E_g + \mu_g I_g \\ (v_b + \mu_b)E_b \\ -v_b E_b + \mu_b I_b \end{bmatrix} = :F(x) - V(x) \quad (15)$$

746 Let F_0 and V_0 be the Jacobian matrices of the six elements of F and V , respectively,
 747 evaluated at the disease-free equilibrium. Then,

$$748 \quad F_0 = \begin{bmatrix} 0 & 0 & 0 & \frac{B_g \beta_h}{K_g} & 0 & \frac{B_b \beta_h}{K_b} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{B_g \beta_g}{H_0} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \frac{B_b \beta_b}{H_0} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} \quad (16)$$

749 and,

$$750 \quad V_0 = \begin{bmatrix} \mu_h + v_h & 0 & 0 & 0 & 0 & 0 \\ -v_h & \mu_h + \gamma_h & 0 & 0 & 0 & 0 \\ 0 & 0 & \mu_g + v_g & 0 & 0 & 0 \\ 0 & 0 & -v_g & \mu_g & 0 & 0 \\ 0 & 0 & 0 & 0 & \mu_b + v_b & 0 \\ 0 & 0 & 0 & 0 & -v_b & \mu_b \end{bmatrix} \quad (17)$$

751 The next generation matrix is

$$752 \quad R = F_0 \cdot V_0^{-1} \quad (18)$$

753 or,

$$\begin{aligned}
 &754 \quad R = \begin{bmatrix} 0 & 0 & \frac{\nu_g \beta_h B_g}{K_g \mu_g (\mu_g + \nu_g)} & \frac{\beta_h B_g}{K_g \mu_g} & \frac{\nu_b \beta_h B_b}{K_b \mu_b (\mu_b + \nu_b)} & \frac{\beta_h B_b}{K_b \mu_b} \\ 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{\nu_h \beta_g B_g}{\zeta} & \frac{\beta_g B_g}{H_0 (\mu_h + \gamma_h)} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \\ \frac{\nu_h \beta_b B_b}{\zeta} & \frac{\beta_b B_b}{H_0 (\mu_h + \gamma_h)} & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 \end{bmatrix} \quad (19)
 \end{aligned}$$

755 where $\zeta = H_0(\mu_h + \nu_h)(\mu_h + \gamma_h)$. The k_{ij} entry of R is the average number of cases in class i
 756 resulting from an infectious individual in class j . Finally, R_0 can be calculated as the absolute
 757 value of the largest eigenvalue, or the spectral radius, of the next generation matrix.

$$\begin{aligned}
 &758 \quad R_0 = \sqrt{\frac{\beta_h B_g \nu_g}{K_g \mu_g (\mu_g + \nu_g)} \cdot \frac{\beta_g B_g \nu_h}{\zeta} + \frac{\beta_h B_b \nu_b}{K_b \mu_b (\mu_b + \nu_b)} \cdot \frac{\beta_b B_b \nu_h}{\zeta}} \quad (20)
 \end{aligned}$$

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923

924 **Supporting Information Legends**

925 **Supplementary Data 1.** The questionnaire used in the preliminary survey.

926 **Supplementary Data 2.** The questionnaire used in the second survey. The human-mosquito
927 contact rates used in the mathematical model analyses were derived from this questionnaire.

928 **Supplementary Table 1.** Selected demographic variables of research participants in three study
929 sites.

930 **Supplementary Figure 1.** A diagram showing the SEIR model compartments and parameters.

931 Black arrows connecting boxes represent the transitions of one disease state to another. Vertical

932 black arrows leaving boxes represent deaths. Vertical black arrows going into boxes represent

933 recruitments of new individuals. Dashed arrows represent contacts between humans and

934 mosquitoes. S_h , S_g , and S_b represent susceptible human, *Ae. aegypti* and *Ae. albopictus*,

935 respectively. E_h , E_g , and E_b represent exposed human, *Ae. aegypti*, and *Ae. albopictus*,

936 respectively. I_h , I_g , and I_b represent infected human, infected *Ae. aegypti*, and *Ae. albopictus*,

937 respectively. R_h represent recovered human. Other parameters are described in Table 1 in the

938 main manuscript.

939 **Supplementary Figure 2.** Bar graphs showing the distributions of research participants' age and
940 gender in the second survey.

941 **Supplementary Figure 3.** Graphs showing the average time spent outside in the past 24 hours
942 during weekday and weekend reported by research participants from ORL and TAM. The unit of
943 time duration on the y-axis is in minutes. The time of the day includes 'morning' (from 06:00 to
944 10:00), 'day' (from 10:00 to 17:00), 'evening' (from 17:00 to 20:00), and 'night' (from 20:00 to
945 06:00 the next day). The error bars represent the standard errors.

946 **Supplementary Table 2.** Results from a quasi-Poisson regression analysis with a log link
947 function to determine the associations between the response variable, the time spent outside
948 between 5 pm to 6 am reported by research participants, and study sites, weekend/weekday
949 setting, and ages and gender of participants.

950 **Supplementary Table 3.** Results from a quasi-Poisson regression analysis with a log link
951 function to determine the associations between the response variable, the numbers of mosquito
952 bites reported by research participants, and time spent outside, the month of data collection, study
953 site, and gender of participants.

954 **Supplementary Figure 4.** The extended sensitivity analysis plots of R_0 to selected model's
955 parameters from the DENV transmission model in ORL. Red points represent the baseline values
956 of the parameters.

957 **Supplementary Figure 5.** The extended sensitivity analysis plots of R_0 to selected model's
958 parameters from the DENV transmission model in TAM. Red points represent the baseline values
959 of the parameters.

