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## RESEARCH

# Parasitism of *Aedes albopictus* by *Ascogregarina taiwanensis* lowers its competitive ability against *Aedes triseriatus*

Emma Stump<sup>1</sup>, Lauren M. Childs<sup>2</sup> and Melody Walker<sup>2\*†</sup>

## Abstract

**Background:** Mosquitoes are carriers for many diseases that significantly impact the human population such as dengue, malaria and La Crosse virus. When multiple mosquito species are present, the competition between species may alter disease spread. Two mosquito species, *Aedes albopictus* and *Aedes triseriatus*, both inhabit areas where La Crosse Encephalitis Virus is found. Infection of *Aedes albopictus* by the parasite *Ascogregarina taiwanensis* can decrease the mosquito's fitness and impact its initial competitive advantage over *Aedes triseriatus*. The decrease in fitness occurs through the impact of *Ascogregarina taiwanensis* on female fecundity, larval development rate, and larval mortality.

**Methods:** In this paper, we examine the effects of parasitism of *Ascogregarina taiwanensis* on *Aedes albopictus* and *Aedes triseriatus* population dynamics and competition. We build a compartmental model using parameters based on published literature, simulate the dynamics of the system, and analyze the effect of parasitism on competition between the mosquito species.

**Results:** We show that increased levels of parasitism in *Aedes albopictus* will decrease the initial competitive advantage of the species over *Aedes triseriatus* and increase the survivorship of *Aedes triseriatus*. An understanding of how population dynamics are affected by this parasite can inform future mosquito control and mosquito-borne disease mitigation efforts.

**Conclusions:** Mosquito population dynamics are affected by many factors, including abiotic factors (e.g. temperature and humidity) and competition between mosquito species. This is especially true when multiple mosquito species are vying to live in the same area. An understanding of mosquito population dynamics is vital to preventing spread of these diseases.

**Keywords:** mosquito population dynamics; competition; *Aedes albopictus*; *Aedes triseriatus*; parasitism; *Ascogregarina taiwanensis*

\* Correspondence: [melody@vt.edu](mailto:melody@vt.edu)

<sup>2</sup>Department of Mathematics, Virginia Tech, 460 McBryde Hall, 225 Stanger Street, 24061 Blacksburg, USA

Full list of author information is available at the end of the article

† Equal contributor



## Background

Mosquito-borne infectious diseases, such as malaria, dengue fever, and La Crosse encephalitis infect millions each year [1, 2]. In particular, *Aedes* mosquitoes, of which there are multiple species, are an important disease vector for dengue, Zika virus,

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7 and La Crosse encephalitis virus (LACV) [3]. We focus on two species known to  
8 transmit LACV, *Aedes albopictus* and *Aedes triseriatus*, and competition between  
9 them.

10  
11 *Aedes albopictus*, also known as the Asian Tiger mosquito, is native to subtropical  
12 regions of southeast Asia, and is a common vector of arboviruses such as Dengue  
13 fever virus, West Nile virus, and La Crosse encephalitis virus [4]. The first appear-  
14 ance of *Ae. albopictus* in the United States was in Houston, Texas in 1985, likely  
15 introduced to the US through the import of used tires [5, 6]. Since its introduction,  
16 *Ae. albopictus* has spread throughout the continental United States, and now oc-  
17 cupies much of the southern and eastern US, stretching from Texas to New Jersey  
18 [7]. *Ae. albopictus* is known for its ability to adapt to a range of climates and to be  
19 a strong competitor to other species that share larval habitats [8].

20  
21 *Aedes triseriatus*, known as the eastern tree hole mosquito, is native to the eastern  
22 United States. *Aedes triseriatus* is the primary vector for the La Crosse virus [9,  
23 10]. La Crosse virus, a pathogen endemic to southwest Virginia, can cause severe  
24 inflammation of the brain [11]. It is primarily zoophilic, but is also known to bite  
25 humans [12]. *Ae. albopictus* will bite both small mammals and humans, making  
26 it more likely to infect human's than *Ae. triseriatus* whose preference is for small  
27 mammals [10].

28  
29 Several laboratory studies have shown that *Ae. albopictus* is the superior com-  
30 petitor compared to *Ae. triseriatus* [13, 14, 15, 16, 17, 18, 19]. In [14], they showed  
31 a ten percent drop in survival for *Ae. triseriatus* when a quarter of the mosquitoes  
32 present were *Ae. albopictus* and a twenty percent drop in *Ae. triseriatus* survival  
33 when half of the mosquitoes were *Ae. albopictus*. In [13], the authors showed that  
34 while the development time of *Ae. albopictus* was not significantly affected by com-  
35 petition, the development time of *Ae. triseriatus* was increased when in a shared  
36 habitat with other *Aedes* species. Moreover, *Ae. albopictus* larvae inhibit egg hatch-  
37 ing of other species such as *Ae. triseriatus*, while there is no significant inhibition  
38 on their own species [15].

39  
40 Both *Ae. albopictus* and *Ae. triseriatus* can be infected by an intestinal proto-  
41 zoan parasite that inhabits the gut of the mosquito throughout its life cycle. The  
42 parasites occur at varying levels in populations of *Aedes* mosquitoes across different  
43 geographical ranges. *Ae. triseriatus* and *Ae. albopictus* are parasitized by *Ascogre-*  
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6 40 *garina barretti* and *Ascogregarina taiwanensis*, respectively [5, 20]. In this work,  
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8 41 we build a mathematical model of *Aedes* population dynamics accounting for par-  
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10 42 asitism of *Ae. albopictus* by *As. taiwanensis*. *As. barretti* impact the fitness of *Ae.*  
11 43 *triseriatus*, but it is mostly dependent on resources availability [20]. In low resources  
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13 44 they find that *Ae. triseriatus* development time is increased significantly, but with  
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15 45 sufficient resources there is not a significant difference. As *Ae. triseriatus* is native  
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17 46 infection with this parasite is assumed to be endemic. We address this by increasing  
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19 47 the development time range found for *Ae. triseriatus*. In the wild, typically 67 to  
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21 48 95% of a given population of *Ae. albopictus* are infected with *As. taiwanensis* [21].  
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23 49 Research indicates that infection of *Ae. albopictus* by *As. taiwanensis* lengthens  
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25 50 larval development time for both males and females mosquitoes, reduces adult fe-  
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27 51 male fecundity, increases larval mortality, and reduces egg laying and hatching rates  
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29 [5, 22].

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32 53 Our model formulation encodes competition by the *Ascogregarina* parasite us-  
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34 54 ing the Lotka-Volterra model, a basis for many inter-specific competition models  
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36 55 [23, 24, 25, 26, 27, 28] including mosquito populations [29, 16, 30, 31]. In [32], a two  
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38 56 species Lotka-Volterra competition model is introduced, which includes reproduc-  
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40 57 tive interference. Analysis of their model showed that reproductive interference is  
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42 58 more likely than limited resources to cause competitive exclusion [33]. The model  
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44 59 was then expanded to include preference in mating for competition between *Ae.*  
45  
46 60 *albopictus* and *Ae. aegypti* [31]. However the type of reproductive interference seen  
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48 61 with *Ae. albopictus* and *Ae. aegypti*, does not seem to be an important factor in  
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50 62 *Ae. albopictus* and *Ae. triseriatus* from the literature. In [16], they compared *Ae.*  
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52 63 *albopictus* and *Ae. triseriatus* using a Lotka-Volterra model to explain possible  
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54 64 competition affects either in tree holes or in tires. This model was then extended  
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56 65 to include La Crosse spread [29].

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59 66 The life of an *Aedes* mosquito consists of 4 stages: egg, larvae, pupae, and adult  
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61 67 (Fig. 1). In total, it takes about 20 days for an individual mosquito to progress from  
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63 68 egg to adult [13]. *Aedes* habitats for egg laying are small and can be anything from  
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65 69 hollow trees to used tires to empty buckets in a suburban yard [34]. From the egg  
70  
71 72 stage, the mosquito progresses through four larval stages and a pupa. The mosquito  
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74 remains in water until it emerges into its adult form [35]. Female mosquitoes begin  
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76 to feed on blood from human or animal hosts so that they may produce eggs. Female

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6 73 mosquitoes require a blood meal in order to lay eggs, and usually lay 100 to 200  
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8 74 eggs at a time. The cycle that a female goes through for each egg batch is known as  
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10 75 the gonotrophic cycle [36]. Female mosquitoes may become vectors for disease when  
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12 76 they feed on infected animal reservoirs and transmit the virus to other animals or  
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14 77 humans via a second blood meal.

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16 78 The life cycle of *As. taiwanensis* mimics that of *Ae. albopictus*: each stage of its  
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18 79 development is analogous to a stage within mosquito development. See the inset into  
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20 80 that of the *Aedes* mosquito in Fig 1. Transmission of *As. taiwanensis* is horizontal  
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22 81 between individuals of *Ae. albopictus*, and does not occur from parent to offspring  
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24 82 [21]. Initial infection occurs when the mosquito larvae ingest oocysts. After inges-  
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26 83 tion, *As. taiwanensis* travels through the midgut, epithelial tissues, and excretory  
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28 84 system of the mosquito, transitioning into different life stages as the mosquito ma-  
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30 85 tures to adulthood. From there, the parasite reproduces and offspring are excreted  
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32 86 by the adult mosquitoes into breeding containers [37].

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34 87 Since new *Ae. albopictus* habitats are unlikely to be contaminated with *Ae. tai-*  
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36 88 *wanensis*, then new populations of *Ae. albopictus* can initially escape parasitism.  
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38 89 This lack of parasite infection in newly established populations gives the mosquito a  
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40 90 potential competitive advantage over *Ae. triseriatus* [5, 21]. Knowledge of how par-  
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42 91 asite infection affects the survivorship of *Ae. albopictus* will provide insight into the  
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44 92 competition between the two mosquito species, and subsequently, help to deepen  
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46 93 understanding of the spread of mosquito-borne infectious disease. In this study,  
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48 94 we examine whether the parasitism of *Ae. albopictus* by *As. taiwanensis* decreases  
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50 95 the mosquito's competitive ability enough to alter the dynamics between the two  
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52 96 *Aedes* mosquitoes. We build a compartmental model of the interactions of the two  
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54 97 mosquito species and *As. taiwanensis*. We parameterize the model from published  
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56 98 literature, simulate dynamics, investigate a wide parameter space, and examine the  
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58 99 effects of parasitism.

## 100 **Methods**

101 We constructed a four compartment model of mosquito population dynamics in-  
102 cluding larval and adult stages of both *Ae. albopictus* and *Ae. triseriatus* (Eq. 1-4).  
103 We simplify the life cycle of the *Aedes* mosquito to just two stages because most,  
104 if not all, of the effects of competition and parasitism are felt at the larval and

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105 adult stages. Furthermore, including all mosquito life stages would unnecessarily  
106 complicate the model. We based our model of competition on the Lotka-Volterra  
107 model of species interaction [38, 39, 40, 41]. We use the Lotka-Volterra model to  
108 incorporate inter-specific competition between the two species and include effects  
109 of parasitism. The effect of parasitism is incorporated in three ways: (i) decreased  
110 fecundity, (ii) increased development time, and (iii) increased larval mortality. This  
111 provides a potential decrease in the competitive advantage of *Ae. albopictus* over  
112 the population of *Ae. triseriatus*.

113 The model includes four compartments: larval *Ae. albopictus* ( $L_a$ ), adult *Ae. al-*  
114 *bopictus* ( $A_a$ ), larval *Ae. triseriatus* ( $L_t$ ), and adult *Ae. triseriatus* ( $A_t$ ). Larval  
115 mosquitoes  $L_i$  are born at rate  $\beta_i$ , die at rate  $\mu_{L_i}$ , and develop at time  $\delta_i$  where  
116  $i \in \{a, t\}$ . Adults emerge from larva at rate  $\delta_i$  and die at rate  $\mu_{A_i}$  where  $i \in \{a, t\}$   
117 for *Ae. albopictus* and *Ae. triseriatus*, respectively. Similar formulations for *Ae. al-*  
118 *bopictus* population dynamics are found in [42]. The parameters  $\rho_a$  and  $\rho_t$  represent  
119 the proportion of adults that are female.  $K$  is the carrying capacity of the larval  
120 population for the two species. Two parameters,  $\alpha_a$  and  $\alpha_t$ , quantify the intrinsic  
121 effect of one species on the other. Parasitism is included through the parameters rep-  
122 resenting effects on female fecundity ( $\gamma_b$ ), larval development rate ( $\gamma_d$ ), and larval  
123 mortality ( $\gamma_m$ ). This forms our system of ordinary differential equations:

$$\frac{dL_a}{dt} = \frac{\beta_a}{\gamma_b} \rho_a A_a \left(1 - \frac{L_a + \alpha_t L_t}{K}\right) - \frac{1}{\gamma_d \delta_a} L_a - \gamma_m \mu_{L_a} L_a, \quad (1)$$

$$\frac{dA_a}{dt} = \frac{1}{\gamma_d \delta_a} L_a - \mu_{A_a} A_a, \quad (2)$$

$$\frac{dL_t}{dt} = \rho_t \beta_t A_t \left(1 - \frac{\alpha_a L_a + L_t}{K}\right) - \frac{1}{\delta_t} L_t - \mu_{L_t} L_t, \quad (3)$$

$$\frac{dA_t}{dt} = \frac{1}{\delta_t} L_t - \mu_{A_t} A_t. \quad (4)$$

124 From a literature search, we determined biologically relevant ranges for parameter  
125 values. A description of the parameters is provided in Table 1. As it was often diffi-  
126 cult to directly find relevant values in the literature, we often needed to transform  
127 values found to meet our parameter descriptions. The birthrate was calculated from  
128 data for gross reproductive rate (GRR) and length of gonotrophic cycle (GC) by  
129 taking the minimum GRR and dividing by the maximum length of the GC. The

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6 130 maximum value was found by dividing the maximum GRR by the minimum GC  
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8 131 length [43]. With this, we calculated a range of 2.5 to 56 eggs laid per adult female  
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10 132 per day. A similar calculation was performed to find a birthrate for *Ae. triseriatus*,  
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12 133 where we calculated a range of 3 to 26 eggs laid per adult female per day [44, 45].  
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14 134 Development time can vary greatly based on a variety of factors and has been found  
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16 135 to be as short as 9 days and as long as 40 days for *Ae. albopictus* [46, 13, 47]. *Ae.*  
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18 136 *triseriatus* has been shown to develop slower than *Ae. albopictus* [13, 18]. In the  
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20 137 model, these values are incorporated directly as development time of larvae, ( $\delta_a$ )  
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22 138 and ( $\delta_t$ ). Larval ( $\mu_{L_a}$ ) and adult ( $\mu_{A_a}$ ) mortality for *Ae. albopictus* were calcu-  
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24 139 lated to be 0.067 and 0.05, respectively, from survival rates and development rates  
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26 140 [46, 43, 13, 47], such that  $\mu = 1 - (\text{survival rate})^\delta$ . For *Ae. triseriatus*, larval ( $\mu_{L_t}$ )  
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28 141 and adult ( $\mu_{A_t}$ ) mortality were found to be 0.011 and 0.1, respectively [48, 49]. The  
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30 142 carrying capacity for the larval population of both species ( $K$ ) was set at 60 as was  
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32 143 found for a study performed in 200ml of water [5]. It is important to note that this  
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34 144 number is relative and could be scaled to fit different size larval containers. In this  
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36 145 study we focus on the proportion of each species such that raw population sizes are  
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38 146 not influential. There is evidence of potential sex imbalance mosquitoes especially  
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40 147 with lower food resources for *Ae. triseriatus*, so the proportion of female,  $\rho_t$ , will  
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42 148 be between 0.2 and 0.6 [17]. In the same study, *Ae. albopictus* had less variation,  
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44 149 0.4 – 0.55, in the proportion females.

45  
46 150 In [16], the competition parameters from the Lotka Volterra model were fit using  
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48 151 nutrient fluids. For the competition parameter of *Ae. albopictus* on *Ae. triseriatus*  
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50 152 ( $\alpha_a$ ) and the competition parameter of *Ae. triseriatus* on *Ae. albopictus* ( $\alpha_t$ ) were  
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52 153 found to be 0.73 and 0.42 in treehole fluid and 0.25 and 0.83 in tire fluid, respectively.  
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54 154 Since *Ae. albopictus* is the superior competitor, we choose a range of [0, 0.75] for  
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56 155 the effect on *Ae. albopictus* from *Ae. triseriatus* and a range of [0.4, 1] for the effect  
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58 156 on *Ae. triseriatus* from *Ae. albopictus*.

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60 157 The effects of parasitism on female fecundity ( $\gamma_b$ ), larval development rate ( $\gamma_d$ ),  
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62 158 and larval mortality ( $\gamma_m$ ) were shown to vary with resource availability. In low re-  
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64 159 sources the effects of parasitism are greater. In [22], they found that in low resources  
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66 160 the mortality of infected *Ae. albopictus* larvae was seven times greater. They also  
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68 161 found that fecundity and fertility was reduced by over 20% as well as development  
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70 162 time was increased by 44%. In [5], they showed that development time of infected

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6 163 *Ae. albopictus* increases with greater interspecific competition with *Ae. triseriatus*.  
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8 164 They saw that without *Ae. triseriatus*, the median development time of infected *Ae.*  
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10 165 *albopictus* was not significantly different. They also found that survival rates were  
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12 166 significantly different for *Ae. triseriatus* at lower densities with *Ae. albopictus*. They  
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14 167 did not observe a significant change in survival for *Ae. albopictus* from parasitism,  
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16 168 but a greater effect from intra- and inter-specific competition. We initially set these  
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18 169 values all to one which represents the case with no parasitism. We then consider  
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20 170 ranges from 1 to 4 for parasite's effect on fecundity and development time and 1 to  
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22 171 8 for mortality. These values were chosen to cover the ranges of changes found in  
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24 172 [22], but we will extend these ranges in farther analyses. If  $\gamma_d = 5$ , this would mean  
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26 173 that the development time was 5 times greater when *Ae. albopictus* is infected with  
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28 174 the parasite. If any of the parasite parameters are set to one this indicates no effect  
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30 175 of parasitism.

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32 176 We simulated the mosquito population dynamics from our ODE model in Matlab.  
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34 177 Fixed parameter values, shown in Table 1, were used in these simulations. The initial  
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36 178 conditions used for all simulations were  $L_a = 30$ ,  $A_a = 0$ ,  $L_t = 30$ , and  $A_t = 0$ . We  
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38 179 use these initial condition as the same conditions as [5], but as we run the simulation  
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40 180 until equilibrium other initial values will give the same results. Simulations were  
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42 181 run for 2000 days, long enough such that the population of *Ae. albopictus* and  
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44 182 *Ae. triseriatus* larvae and adults reached equilibrium. To begin we considered two  
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46 183 competition scenarios. The first is the environment within a tire, which  $\alpha_a$  and  $\alpha_t$   
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48 184 were fixed at 0.83, and 0.25 respectively, which would indicate that *Ae. albopictus*  
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50 185 has more effect on *Ae. triseriatus*. In the second scenario the environment would  
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52 186 be in a treehole with  $\alpha_a = 0.42$  and  $\alpha_t = 0.73$ , so that *Ae. triseriatus* has a greater  
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54 187 effect on *Ae. albopictus*. These parameters were from fitted data in [16].

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56 188 We performed a parameter sweep by sampling ranges of the parameters using  
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58 189 Latin Hypercube sampling (LHS) in Matlab [50]. We conducted this with a sample  
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60 190 size of 100,000, and sampled 12 of the parameters:  $\beta_a$ ,  $\beta_t$ ,  $\delta_a$ ,  $\delta_t$ ,  $\mu_{L_t}$ ,  $\mu_{A_t}$ ,  $\mu_{L_a}$ ,  
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62 191  $\mu_{A_a}$ ,  $\alpha_t$ ,  $\alpha_a$ ,  $\rho_t$ , and  $\rho_a$ . Values for parasitism ( $\gamma_b$ ,  $\gamma_d$ ,  $\gamma_m$ ) were fixed at 1, and  $K$   
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64 192 was fixed at 60. With the results generated by the LHS, we generated a histogram  
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193 reflecting the outcomes of the one hundred thousand samples. We categorized the  
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195 results into seven outcomes, described in Table 2. These categories were based on  
the proportion of the population occupied by *Ae. albopictus* as follows: In category



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6 196 (1), a proportion of less than 0.01; in category (2), a proportion of 0.01 to 0.2; in  
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8 197 category (3), a proportion between 0.2 and 0.4; in category (4), a proportion between  
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10 198 0.4 and 0.6; in category (5), a proportion between 0.6 and 0.8; In category (6), a  
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12 199 proportion between 0.8 and 0.99; and in category (7) a proportion is greater than  
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14 200 0.99. We then did a sensitivity analysis on the parameters to account for uncertainty  
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16 201 and variation in parameters by the way of partial rank correlation coefficient [51].

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18 202 After sampling the space of the twelve parameters in the model in the absence of  
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20 203 parasitism, we focused on investigating the effects of the parasite. We repeated the  
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22 204 LHS with the parasite parameter varied and displayed this in a histogram as well.  
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24 205 We also performed sensitivity analysis on the 100,000 LHS samples that includes  
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26 206 varied parasite effects. The mortality and fecundity parasite parameter were varied  
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28 207 from 1 to 4 and the development time parasite parameter varied from 1 to 8, where a  
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30 208 value of 1 means the parasite has no effect and a value of 3 means a 3 fold increased  
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32 209 effect of parasitism. This means that mortality or development time is increased or  
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34 210 fecundity is decreases compared to the expected value without parasitism.

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36 211 To examine the varying effects of parasitism fixed all parameters as listed in Table  
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38 212 1 except we varied the three parasite parameters. We compared effects on female  
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40 213 fecundity, larval development rate, and larval mortality to see how these different  
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42 214 combinations led to different outcomes in terms of the proportion *Ae. albopictus* in  
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44 215 the final population. We extended the range of the parasite parameters so that all  
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46 216 were varied from 1 to 10.

## 47 **Results**

48  
49 218 To begin, we model the population dynamics of *Ae. albopictus* and *Ae. triseriatus*  
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51 219 without parasitism. We consider two separate environments: tire and treehole. The  
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53 220 difference between the two is the competition parameters ( $\alpha_t$  and  $\alpha_a$ ) that were fit  
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55 221 for each environment from [16]. In both cases, the populations settle to an equilib-  
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57 222 rium. The results in the tire environment land in category 6, in which *Ae. albopictus*  
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59 223 dominates, but *Ae. triseriatus* remain at low levels (Fig. 2, right). After 150 days,  
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61 224 we find 126 adult *Ae. albopictus* compared to about 5 adult *Ae. triseriatus*. The  
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63 225 results for the treehole environment land in category 5 (Fig. 2 left), where *Ae. al-*  
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65 226 *bopictus* is still the dominant species, but *Ae. triseriatus* has a sizeable population.  
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67 227 After 150 days, there are approximately 54 *Ae. albopictus* and 19 *Ae. triseriatus*.

228 Parameter values are an estimated averages from literature and are found in Table  
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230 To account for known variability in parameters, we examined dynamics across  
231 broad parameter space using a Latin hypercube sampling (LHS) with the ranges  
232 indicated in Table 1. Assuming no effects of parasitism, we find that the majority,  
233 56%, of simulations fall into category 6 (Fig. 3, left), which is the same as the tire  
234 scenario, where *Ae. albopictus* strongly dominates. In addition, approximately 25%  
235 of the simulations fall into the same category as the treehole scenario (category 5).  
236 Only 3.46% of the total 100,000 samples led to categories in which *Ae. triseriatus* is  
237 greater in population than *Ae. albopictus* (categories 1, 2 and 3). A further 10.6%  
238 of the simulation fell into coexistence with approximately equal amounts of both  
239 species (category 4). For a small number of simulations *Ae. albopictus* completely  
240 eliminated *Ae. triseriatus* without parasitism (5%), but the most common scenario  
241 was for *Ae. albopictus* to be the dominant species and strongly limit the population  
242 of *Ae. triseriatus*.

#### 243 Including parasitism

244 When we include the effects of parasitism in the dynamics, we greatly increase the  
245 parameter space where *Ae. triseriatus* is the dominant species. Here, we again use  
246 LHS but include the parameters for parasitism:  $\gamma_d$ ,  $\gamma_m$ , and  $\gamma_b$ . We find that results  
247 falling in categories one to four have greatly increased while those in categories  
248 six and seven have significantly decreased (Fig. 3, right). In fact, *Ae. albopictus*  
249 complete eliminates *Ae. triseriatus* in less than 1% of the simulations (category  
250 7). Rather, 44.29% of the time *Ae. triseriatus* is the dominant species (category  
251 1,2,3) and only 39.95% of the time that *Ae. albopictus* will be the dominant species  
252 (category 5,6,7). The categories with the most outcomes including parasitism are  
253 categories 1,6 and 5 with 21.39%, 20.07%, and 19.36%, respectively. Overall we see  
254 that without parasitism, *Ae. albopictus* will be the dominant vector, however once  
255 parasitism takes place *Ae. triseriatus* can become dominant.

256 To further examine the effects of parasitism, we vary the level of each of the three  
257 parasitism parameters. We perform these variations pairwise under two environ-  
258 mental scenarios: tire (Fig. 5 a-g) and tree hole (Fig. 6 a-g). Recall, the difference  
259 between the two scenarios is the competition parameters ( $\alpha_t$  and  $\alpha_a$ ) from [16].

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6 260 In the tire scenario, the competition effect of *Ae. albopictus* on *Ae. triseriatus* is  
7  
8 261 greater ( $\alpha_a = 0.83 > 0.25 = \alpha_t$ ) and for the treehole scenario, the competition  
9  
10 262 effect of *Ae. triseriatus* on *Ae. albopictus* is greater ( $\alpha_a = 0.42 < 0.73 = \alpha_t$ ). All  
11 263 other parameters are fixed (Table 1). The colors in these images correspond to the  
12  
13 264 colors the seven categories from Table 2, although only six colors appear as category  
14  
15 265 7 never occurs in these simulations. Parasitism effects were varied pairwise. First,  
16  
17 266 parasite effects on larval mortality ( $\gamma_m$ ) and larval development time ( $\gamma_d$ ) were var-  
18  
19 267 ied with three constant levels of the effect on female fecundity ( $\gamma_b = 1, 3, 5$ ) (Fig. 5  
20  
21 268 a-c and 6 a-c). Then, parasite effects on larval mortality ( $\gamma_m$ ) and female fecundity  
22  
23 269 ( $\gamma_b$ ) were varied with three constant levels of the effect on larval development time  
24  
25 270 ( $\gamma_m = 1, 3, 5$ ) (Fig. 5 e-g and 6 e-g). Finally, parasite effects on female fecundity  
26  
27 271 ( $\gamma_b$ ) and larval development time ( $\gamma_d$ ) were varied with three constant levels of the  
28  
29 272 effect on mortality ( $\gamma_m = 1, 3, 5$ ). This is not shown as effects on development time  
30  
31 273 and fecundity are similar to effects on development time and mortality.

32  
33 274 In the tire scenario ( $\alpha_a = 0.83 > 0.25 = \alpha_t$ ), we find that in large portions of  
34  
35 275 parameter space *Ae. albopictus* strongly dominates, i.e. category six (Fig. 5, dark  
36  
37 276 yellow). When the effect on female fecundity ( $\gamma_b$ ) is fixed at one, the transition to a  
38  
39 277 greater level coexistence between the mosquito species is only seen at higher levels  
40  
41 278 of effects on larval development rate ( $\gamma_d$ ), with values around  $\gamma_d > 5$  (Fig. 5 a).  
42  
43 279 For female fecundity ( $\gamma_b$ ) fixed at three and five (Figure 5 b,c), development time  
44  
45 280 effects as low as  $\gamma_d \approx 3$  and  $\gamma_d \approx 2.5$  result in a shift low levels of *Ae. albopictus*,  
46  
47 281 but still the dominant species, i.e. category 5 in green. In order for *Ae. triseriatus*  
48  
49 282 to be the dominant species there must be very high effects of all three parameters.

50  
51 283 Parasite effects on development time have more significant effects than on mor-  
52  
53 284 tality or fecundity. This is most apparent when there is no change in development  
54  
55 285 time (Fig. 5 e), then *Ae. albopictus* always strongly dominates. In other words, there  
56  
57 286 is no change in category, regardless of the strength of the effect on mortality and  
58  
59 287 fecundity. If the effect on development time is increased by three times (Figure 5 f),  
60  
61 288 both effects on fecundity and mortality must be relatively high to get higher levels  
62  
63 289 of *Ae. triseriatus*. Furthermore, *Ae. triseriatus* will only be more dominant if both  
64  
65 290 parasite effects on fecundity and mortality are greater than ten. When development  
66  
67 291 time is five times greater, only a small effect by the other two parameters is needed  
68  
69 292 to decrease the proportion of *Ae. albopictus* to category 5. Similarly, with fixed

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6 293 fecundity, when the parasite increases the development time seven fold, we see that  
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8 294 regardless of the other two parameters, the proportion of *Ae. albopictus* decreases  
9  
10 295 to at minimum category 5 (Fig. 5 a-c, green and blue).

11 296 In the treehole scenario where *Ae. triseriatus* has a more competitive effect on *Ae.*  
12  
13 297 *albopictus* (Fig. 6). As seen with the absence of parasitism, the default is category  
14  
15 298 5 (Fig. 6 a and e, green in bottom left corner), in which *Ae. albopictus* is still the  
16  
17 299 dominant species, but there are a larger number of *Ae. triseriatus*. In this situations,  
18  
19 300 the effect on development time must only increase two-fold for the proportion of *Ae.*  
20  
21 301 *albopictus* to decrease to category 4 (Fig. 6 a-c, teal), in which there are relatively  
22  
23 302 similar amounts of both species. When the effect on fecundity set to 3 (Fig. 6 b)  
24  
25 303 and the effect of development time is greater than four *Ae. triseriatus* will be the  
26  
27 304 dominant species (all three shades of blue). When the effect of fecundity is set to 5  
28  
29 305 (Fig. 6 c) and the development time is above three, *Ae. triseriatus* will dominate.  
30  
31 306 A similar result is seen when development time is five times greater (Fig. 6 c). For  
32  
33 307 all values of the other two parameters, *Ae. triseriatus* is the dominant species. In  
34  
35 308 fact, almost half of the parameter space considered falls into category 1 where *Ae.*  
36  
37 309 *albopictus* is eliminated (darkest blue). Without any parasite effects on development  
38  
39 310 time (Fig. 6 e) there is only a chance for the two species to be relatively equal if  
40  
41 311 both other parameters are greater than 7.

42  
43 312 Only with very high effects on all three parameters do we find that *Ae. albopictus*  
44  
45 313 is dominated by *Ae. triseriatus*. However, in both scenarios, as we increase the effects  
46  
47 314 of the parasite parameters we see that the proportion of *Ae. albopictus* decreases.  
48  
49 315 The change is most notable as the parasite effect on *Ae. albopictus* development  
50  
51 316 time is increased, regardless of the scenario.

#### 52 317 Importance of parameters

53 318 From the LHS, we look at the partial rank correlation coefficient (PRCC) for each  
54  
55 319 parameters. We consider how each parameter effects the proportion of *Ae. albopictus*  
56  
57 320 after 2000 days. In the case without parasitism, we find that almost all parameters  
58  
59 321 have a significant impact on the model except the parameters for the death of  
60  
61 322 *Ae. triseriatus* larvae  $\mu_{L_t}$ , (Fig. 4, top row). When parasitism is included (Fig.  
62  
63 323 4, bottom row), the parameters which are not significant are all related to *Ae.*  
64  
65 324 *triseriatus*: death of larvae,  $\mu_{L_t}$ ; proportion of females,  $\rho_t$ ; and the birth rate,  $\beta_t$ .

325 In the case without parasitism, the parameter with the most influence (largest  
 326 PRCC value in magnitude) is the competition parameter  $\alpha_a$ , which is the inter-  
 327 specific competition effects on *Ae. triseriatus* from *Ae. albopictus*, with a PRCC  
 328 value of 0.8455. The more  $\alpha_a$  increases the greater proportion of *Ae. albopictus*.  
 329 There are several parameters which have fairly large correlation. The following  
 330 parameters all have a PRCC value greater than 0.5 in magnitude (in the order  
 331 of greatest magnitude to lowest): death rate of adult *Ae. albopictus*,  $\mu_{A_a}$ ; *Ae. al-*  
 332 *bopictus* larval development time,  $\delta_a$ ; *Ae. triseriatus* larval development time,  $\delta_t$ ,  
 333 the competition parameter  $\alpha_t$  on *Ae. albopictus*; and death rate of adult *Ae. tris-*  
 334 *eriatus*,  $\mu_{A_t}$ . We see that the most important parameters are the death rates of  
 335 adults, transition rate to adults, and the competition parameters.

336 When we introduce parasitism parameters into the LHS, we see that the para-  
 337 site's effect on development time  $\gamma_d$  has the fourth greatest impact with a PRCC of  
 338  $-0.1825$ , so we expect the increase of  $\gamma_d$  to decrease the proportion of *Ae. albopictus*.  
 339 The death of adult *Ae. albopictus*, *Ae. albopictus* larval development time  $\delta_a$ , and  
 340 *Ae. albopictus* birth rate  $\beta_a$ , all have greater PRCC values in magnitude than  $\gamma_d$   
 341 ( $-0.2462$ ,  $-0.2045$ ,  $0.1950$  respectively). This indicates the importance of  $\gamma_d$  relative  
 342 to the other parasitism parameters, although the other two parasite parameters  
 343 are statistically significant ( $p < 0.00001$ ) as well. The PRCC value for the para-  
 344 site's effect on mortality is  $-0.1241$  and the for the parasite's effect on fecundity is  
 345  $-0.0944$ .

#### 346 Analytical formulation of proportion of *Ae. albopictus*

347 We analyzed our model to determine the long term behavior for the proportion of  
 348 *Ae. albopictus*. From the system of equations there are four possible equilibrium:  
 349 extinction of mosquitoes, competitive exclusion with each species type present, and  
 350 coexistence. The equilibrium equations can be found in the supplementary mate-  
 351 rial. Before we discuss our formula for the population proportion, we introduce the  
 352 ratio which represents the reproduction number of each species,  $R_t$  and  $R_a$ , for *Ae.*  
 353 *triseriatus* and *Ae. albopictus*, respectively. These are given by:

$$\begin{aligned}
 R_a &= \frac{\beta_a \rho_a}{\gamma_b} \frac{1}{\mu_{A_a}} \frac{\frac{1}{\gamma_d \delta_a}}{\frac{1}{\gamma_a \delta_a} + \gamma_m \mu_{L_a}}, \\
 R_t &= \beta_t \rho_t \frac{1}{\mu_{A_t}} \frac{\frac{1}{\delta_t}}{\frac{1}{\delta_t} + \mu_{L_t}}.
 \end{aligned}$$

354 In each reproduction number, the first term is the the birth rate,  $\frac{\beta_a \rho_a}{\gamma_b}$  for *Ae.*  
 355 *albopictus* and  $\beta_t \rho_t$  for *Ae. triseriatus*. This is multiplied by the inverse of adult  
 356 death rate, i.e. the expected life span of an adult mosquito. Together, these terms  
 357 are the total expected number of eggs a female we lay in her life time. The final  
 358 term has the development rate, i.e.  $\frac{1}{\delta_t}$  and  $\frac{1}{\gamma_d \delta_a}$ , respectively, divided by the sum of  
 359 the development rate and death rate of larvae. This proportion is the probability  
 360 of an egg surviving to adulthood. Overall, the reproductive number gives the total  
 361 surviving children that a single female will lay. If  $R_t > 1$ , the population of *Ae.*  
 362 *triseriatus* can establish. Similarly, if  $R_a > 1$ , *Ae. albopictus* can establish.

363 We determine the equilibrium for coexistence in terms of  $R_t$  and  $R_a$  (see supple-  
 364 mental material). From these we calculate the equilibrium proportion of adult *Ae.*  
 365 *albopictus* by:

$$\frac{A_a}{A_a + A_t} = \frac{w_d \left(1 - \alpha_t + \frac{\alpha_t}{R_t} - \frac{1}{R_a}\right)}{w_d \left(1 - \alpha_t + \frac{\alpha_t}{R_t} - \frac{1}{R_a}\right) + q_d \left(1 - \alpha_a + \frac{\alpha_a}{R_a} - \frac{1}{R_t}\right)}$$

366 where

$$w_d = \frac{1}{\gamma_d \delta_a \mu_{A_a}},$$

$$q_d = \frac{1}{\delta_t \mu_{A_t}}.$$

367 Notice that the parameters  $w_d$  and  $q_d$  are the inverse of the quantity of develop-  
 368 ment time multiplied by the adult death for *Ae. albopictus* and *Ae. triseriatus*,  
 369 respectively. This represents the expected life span. From our analytical description  
 370 of the proportion of *Ae. albopictus*, we can determine the importance of different  
 371 parameters.

## 372 Discussion

373 Realistically, the combined effects of the parasite would likely not result in complete  
 374 elimination of *Ae. albopictus*. While many studies show that *Ae. albopictus* is the  
 375 stronger competitor, consistently eggs of both species are found together in the wild  
 376 even in the presence of high levels of parasitism [9, 5, 22, 52]. It is unlikely that  
 377 *Ae. triseriatus* would dominate *Ae. albopictus* without significant drastic effects of  
 378 parasitism on the mosquito species. High levels of infection of *Ae. albopictus* with  
 379 *As. taiwanensis* have a significant effect on the population levels and would likely

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6 380 level the playing field between the two mosquito species. Our model demonstrates  
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8 381 this effect with many more situations in which *Ae. triseriatus* is the dominant  
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10 382 species in the presence of parasitism of *Ae. albopictus*.

11 383 There are additional factors other than the effects of *gregarine* parasites, that  
12  
13 384 contribute to coexistence. One of these is that the competitive effects are lessened  
14  
15 385 when resources are sufficient [17]. Although *Ae. triseriatus* develops slower and has  
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17 386 a smaller survival rate, it can survive at a lower temperature than *Ae. albopic-*  
18  
19 387 *tus* [18]. We also make the assumption that the reproductive cycles and seasons  
20  
21 388 of the two *Aedes* mosquitoes overlap completely. However, the populations of the  
22  
23 389 two mosquitoes peak at different times: *Ae. triseriatus* peaks in late June and early  
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25 390 July, while *Ae. albopictus* peaks in late July through late August [9], which could  
26  
27 391 give *Ae. triseriatus* a slight edge that is not incorporated into this model. Because  
28  
29 392 most scenarios resulted in strong domination of *Ae. albopictus*, it is unlikely that  
30  
31 393 this slight edge would cause any significant alterations for most of the season. It  
32  
33 394 would be possible to study these alterations by changing the initial conditions of  
34  
35 395 the simulations. For example, changing the initial conditions so that *Ae. triseriatus*  
36  
37 396 starts with both adults and larvae and *Ae. albopictus* starts only with larvae. Ad-  
38  
39 397 ditionally, we could simulate a later introduction of *Ae. albopictus* to compensate  
40  
41 398 for this difference.

39 399 We also assume that infection of *Ae. triseriatus* by its parasite *Ascogregarina bar-*  
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41 400 *retti* has a slight impact on development time of *Ae. triseriatus*. *Ae. triseriatus* is  
42  
43 401 native to the areas in which it competes with *Ae. albopictus*, and is subsequently  
44  
45 402 unable to escape its parasite in the same way as *Ae. albopictus*. Consequently, high  
46  
47 403 levels of parasitism are assumed to be occurring when the population at equilibrium.  
48  
49 404 Thus, *As. barretti* and its impacts on *Ae. triseriatus* are not included in this model.  
50  
51 405 Additional evidence suggests that *Ae. triseriatus* that are infected with *Ascogre-*  
52  
53 406 *garina barretti* were killed less often by a predator, *Toxohrynychites rutilus*, than  
54  
55 407 compared to uninfected *Ae. triseriatus* [53]. This shows that while the effect of the  
56  
57 408 parasite does have an effect on the competition between the two species, there are  
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59 409 other species which might exacerbate or mitigate the effects of *As. taiwanensis* on  
60  
61 410 *Ae. albopictus*.

60 411 Evidence suggesting that endemic infection of *Ae. albopictus* by *As. taiwanen-*  
61  
62 412 *sis* decreases fitness has implications in the spread of mosquito-borne diseases. In  
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6 413 southwest Virginia, both *Aedes* species can act as a vector for La Crosse encephali-  
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8 414 tis virus (LACV). While *Ae. triseriatus* is the primary vector of the for the virus,  
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10 415 evidence suggests that as *Ae. albopictus* becomes more established, it can transmit  
11  
12 416 LACV just as effectively as *Ae. triseriatus* [5]. Importantly, as *Ae. albopictus* often  
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14 417 occurs in urban or para-urban settings, it can act as a bridge vector for LACV to  
15  
16 418 the human population. While La Crosse encephalitis is not widespread across the  
17  
18 419 US, it one of the most common mosquito-borne pediatric diseases in the country  
19  
20 420 [54]. LACV infections result in inflammation of the brain, which can lead to seizures  
21  
22 421 and paralysis [11]. In the future, this understanding of mosquito population dynam-  
23  
24 422 ics can be implemented in the study of mosquito-borne diseases such as La Crosse  
25  
26 423 encephalitis.

## 424 Conclusion

425 We aimed to determine the extent that parasitism of *Ae. albopictus* by *As. tai-*  
426  
427 426 *wanensis* impacts its competition with *Ae. triseriatus*. Both *Aedes* mosquitoes are  
428  
429 427 potentially competent vectors for a number of human arboviruses, and insight in the  
430  
431 428 dynamics of these two species could help inform future disease mitigation efforts.  
432  
432 429 Without parasitism due to *As. taiwanensis*, *Ae. albopictus* has a large and distinct  
433  
433 430 competitive advantage over *Ae. triseriatus* in many environments. *Ae. albopictus*  
434  
434 431 is an often-invasive generalist species, so its domination over native *Ae. triseriatus*  
435  
435 432 without parasitism is expected. From our parameter sweep conducted via the Latin  
436  
436 433 hypercube sampling, 86% of the scenarios resulted in *Ae. albopictus* being the dom-  
437  
437 434 inant species, with few scenarios leading to *Ae. triseriatus* as the dominant species.  
438  
438 435 This suggests that the competitive advantage of *Ae. albopictus* is so great that if  
439  
439 436 the species has even the slightest edge over *Ae. triseriatus*, it will dominate given  
440  
440 437 enough time. Even in treeholes where the competition effect from *Ae. triseriatus*  
441  
441 438 is greater, *Ae. albopictus* is the dominant species. This is consistent with previ-  
442  
442 439 ous results [5, 16, 22]. Our results indicate that parasitism of *Ae. albopictus* by  
443  
443 440 *As. taiwanensis* decreases overall fitness of the species, and negatively impacts its  
444  
444 441 competitive ability. To be clear, the reduction of individual traits is assumed, but  
445  
445 442 our results indicated that the overall population levels are significantly affected by  
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446 443 changes in these individual traits. This is shown when changing levels of the para-  
447  
447 444 site parameters affect the course of the competition between *Ae. albopictus* and *Ae.*



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6 445 *triseriatus*. The three parameters all have significant effects on the dynamics of the  
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8 446 two species, with parasites effect on development time having the strongest effect  
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10 447 on the proportion of *Ae. albopictus*. The greatest effect on the population dynamics  
11  
12 448 of the two species is observed when there is a combined effect on female fecundity,  
13  
14 449 larval development time, and larval mortality.

#### 15 450 Availability of data and materials

16  
17 451 The datasets generated during the current study are available in its additional files.

#### 18 19 20 452 Abbreviations

21  
22 453 **Ae.:** *Aedes*

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24 454 **LACV:** La Crosse encephalitis virus

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26 455 **PRCC:** partial regression correlation coefficients.

27  
28 456 **As.:** *Ascogregarina*

29  
30 457 **GRR:** Gross reproductive rate

31  
32 458 **GC:** Gonotrophic cycle

#### 33 34 459 **Ethical declarations**

35 460 Ethics approval and consent to participate

36 461 Not applicable.

37  
38  
39 462 Consent for publication

40 463 Not applicable.

41  
42 464 Competing interests

43 465 The authors declare that they have no competing interests.

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#### 51 52 471 **Author's Information**

53 472 Contribution

54 473 Emma Stump developed the model, determined the parameter values, ran initial simulations, developed initial code

55 474 and drafted the manuscript. Melody Walker developed the model and code, analyzed the model, performed

56 475 simulations, and revised the manuscript. Lauren Childs oversaw model development and analysis and edited the

57 476 manuscript.

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60 477 Corresponding Author

61 478 Correspondence to Melody Walker  
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479 **Author details**

480 <sup>1</sup>Systems Biology, Virginia Tech, Hahn Hall South Suite 2108, 24061 Blacksburg, USA. <sup>2</sup>Department of  
481 Mathematics, Virginia Tech, 460 McBryde Hall, 225 Stanger Street, 24061 Blacksburg, USA.

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604 **Figures**

**Figure 1 Lifecycle of the mosquito and parasite.** Interaction between lifecycles of *Aedes* mosquito, shown as the black lines, and *Ascogregarina* parasite, shown as the blue boxes. As the mosquito progresses from stage to stage in its lifecycle, its gregarine parasite progresses through in a mirrored fashion.

**Figure 2 Population distribution over time with fixed parameters.** Expected results without any parasitism in *Ae. albopictus*. When *Ae. albopictus* initially invades a new habitat. All parameters are chosen to be the values in Table 1 with all parasite parameters set to 1. The figure in the left is the tire scenario with competition parameters favoring *Ae. albopictus* ( $\alpha_t = 0.25 < \alpha_a = 0.83$ ). The figure on the right is competition parameters that favor *Ae. triseriatus* ( $\alpha_t = 0.73 > 0.42 = \alpha_a$ ).

**Figure 3 Competition Outcomes in Latin Hypercube Sampling.** The outcomes of competition with the 100,000 samples from the Latin hypercube sampling. The categories shown in dark blue has *Ae. albopictus* ( $A_a$ ) wiped out and the bright yellow is when *Ae. albopictus* completely dominates *Ae. triseriatus*. On the left is without the effects of parasitism on *Ae. albopictus* and the right includes parasitism effects. Categories are defined in Table 2.

**Figure 4 Partial rank Correlation coefficients of the parameter values.** This shows the results of PRCC on the parameter values with stars indicating significance with a p-value less than 0.00001. The top plot shows the PRCC with the LHS with all parasitism parameters set to one ( $\gamma_d = \gamma_m, \gamma_b = 1$ ), indicating no parasitism. The bottom plot is the PRCC with variation of parasitism included in the LHS. Red bars (left side) are parameters associated with *Ae. albopictus* and blue bars (right side) with *Ae. triseriatus*. Parasitism parameters, which only occur in the bottom plot, are shown by purple bars (middle). For each grouping, parameters are ordered from least to greatest from the LHS including parasitism.

**Figure 5 Effects of parasitism on *Ae. albopictus*.** The proportion of *Ae. albopictus* when varying parasitism parameters. All figures have competition parameters  $\alpha_a = 0.83$  and  $\alpha_t = 0.25$ , which means that the effect on *Ae. triseriatus* is greater than on *Ae. albopictus*. The competition parameters were fit in tire fluids [16]. All three parasitism parameters –  $\gamma_b$ ,  $\gamma_m$ ,  $\gamma_d$  – are varied. Across row one and three, the parasitism parameter not on the x or y-axis is fixed at 1, 3, and 5 from left to right. The first row varies the parasites effect on development time (x-axis) and fecundity (y-axis) with the parasites effect on mortality changing from 1, 3 to 5 from left to right. The third rows show effects of fecundity (x-axis) and effects of mortality (y-axis) with effects on development time being 1, 3, and 5 from left to right. The effects of development time verses mortality is very similar to effects on development time versus effects on fecundity (not shown). The figure in the second row is a three dimensional version of the contour lines with effects on mortality on the z-axis, and effects of fecundity on the x-axis. Notice that the effect on development time on the y-axis has been rotated so that the it goes from largest to smallest. Each contour value is listed in the legend (yellow is when the proportion of *Ae. albopictus* equals 0.8). All values to the right of the contour lines correspond to the same color on the 2D contour plots.

**Figure 6 Effects of parasitism on *Ae. albopictus*** The proportion of *Ae. albopictus* when varying parasitism parameters. For all figures, the competition parameters are  $\alpha_a = 0.42$  and  $\alpha_t = 0.73$ . The competition parameters were fit from tree fluids [16]. All three parasitism parameters –  $\gamma_b$ ,  $\gamma_m$ ,  $\gamma_d$  – are varied. Across each row, the parasitism parameter not on the x or y-axis is fixed at 1, 3, and 5 from left to right. The first row varies the parasites effect on development time (x-axis) and fecundity (y-axis) with the parasites effect on mortality changing from 1, 3 to 5 from left to right. The third rows show effects of fecundity (x-axis) and effects of mortality (y-axis) with effects on development time being 1, 3, and 5 from left to right. The effects of development time verses mortality is very similar to effects on development time versus effects on fecundity (not shown). The figure in the second row is a three dimensional version of the contour lines with effects on mortality on the z-axis, and effects of fecundity on the x-axis. Notice that the effect on development time on the y-axis has been rotated so that the it goes from largest to smallest. Each contour value is listed in the legend (green is when the proportion of *Ae. albopictus* equals 0.6). All values to the right of the contour lines correspond to the same color on the 2D contour plots.

## 605 Tables

Table 1 Parameter Values and Latin Hypercube sampling ranges.

<i>Aedes albopictus</i>					
Symbol	Description	Value	LHS Range	Units	Reference
$\beta_a$	Birth Rate	32.6	2.5 – 56	Eggs/day	[43]
$\delta_a$	Development Time	10	9-45	1/days	[46, 13, 47]
$\mu_{L_a}$	Larval mortality	0.067	0.005 – 0.4	1/day	[13, 43]
$\mu_{A_a}$	Adult mortality	0.045	0.01 – 0.065	1/day	[46, 43, 47]
$\alpha_a$	Competition parameter	0.83, 0.42	0.4 - 1	unitless	[16]
$\rho_a$	Adult female proportion	0.5	0.2 - 0.6	unitless	[17]
<i>Aedes triseriatus</i>					
Symbol	Description	Value	LHS Range	Units	Reference
$\beta_t$	Birth rate	11	3 – 26	Eggs/day	[45, 44, 49]
$\delta_t$	Development time	25	13 - 55	1/days	[13, 18, 55],
$\mu_{L_t}$	Larval mortality	0.011	0.002 – 0.011	1/day	[13, 47, 17]
$\mu_{A_t}$	Adult mortality	0.1	0.03 – 0.1	1/day	[48]
$\alpha_t$	Competition Parameter	0.25, .73	0 - 0.75	unitless	[16]
$\rho_a$	Adult female proportion	0.5	0.4 - 0.55	unitless	[17]
Other Parameters					
Symbol	Description	Value	LHS Range	Units	Reference
$\gamma_b$	Effect on fecundity	1.0	1 - 4	unitless	varied
$\gamma_d$	Effect on development rate	1.0	1 - 8	unitless	varied
$\gamma_m$	Effect on larval mortality	1.0	1 - 4	unitless	varied
$K$	Carrying capacity	60	Fixed	Number of larvae	[16]

## 606 Tables

**Table 2 Categorized outcomes.** #Criteria is proportion of *Ae. albopictus* adults.

Category	Description	Criteria# ( $A_a$ )
1	<i>Ae. triseriatus</i> completely dominates, <i>Ae. albopictus</i> wiped out	$A_a < 0.01$
2	<i>Ae. triseriatus</i> dominates, few <i>Ae. albopictus</i> remain	$0.01 < A_a < 0.15$
3	<i>Ae. triseriatus</i> more present, <i>Ae. albopictus</i> still persists	$0.20 < A_a < 0.40$
4	Both species coexist in even proportions	$0.40 < A_a < 0.60$
5	<i>Ae. albopictus</i> more present, <i>Ae. triseriatus</i> persists	$0.60 < A_a < 0.80$
6	<i>Ae. albopictus</i> dominates, few <i>Ae. triseriatus</i> remain	$0.80 < A_a < 0.99$
7	<i>Ae. albopictus</i> completely dominates, <i>Ae. triseriatus</i> wiped out	$A_a > 0.99$



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607 **Additional Files**

608 Additional file 1 — Equilibrium

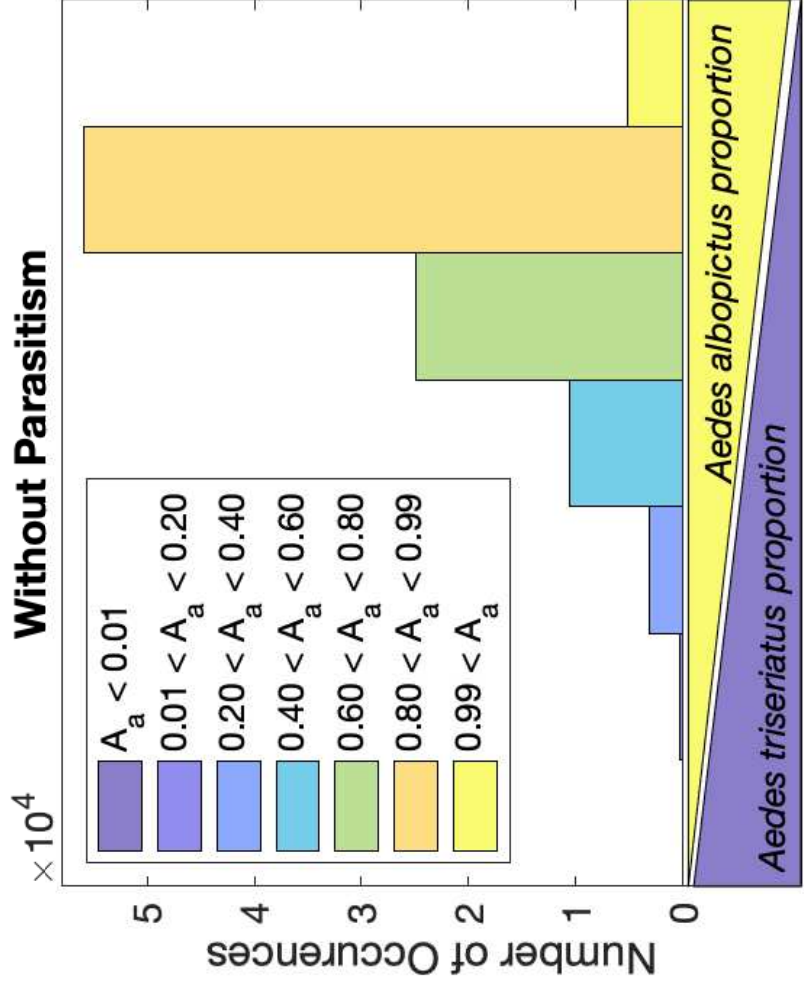
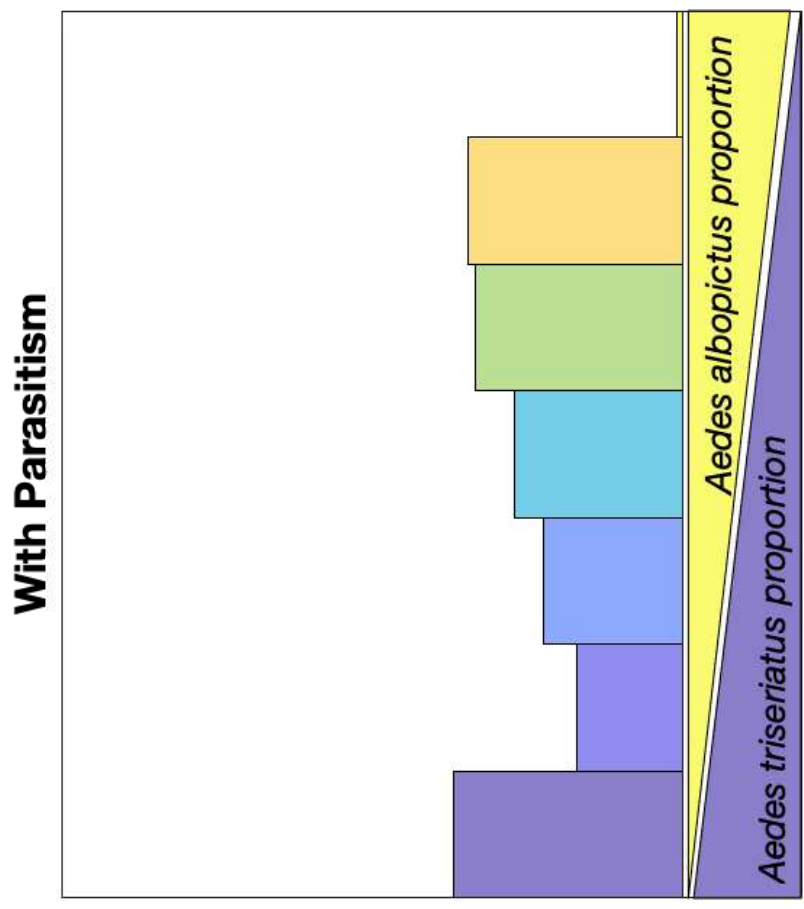
609 This contains the equilibria values. File format is pdf.

610 Additional file 2 — Code

611 This is all the code used to run and analyze the model. File format is Matlab file (.m).

612 Additional file 3— Generated data

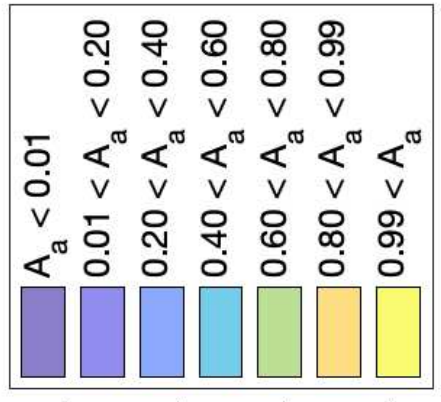
613 This is the all generated samples. The format is a Matlab file (.mat).



× 10<sup>4</sup>

Without Parasitism

With Parasitism



Number of Occurrences

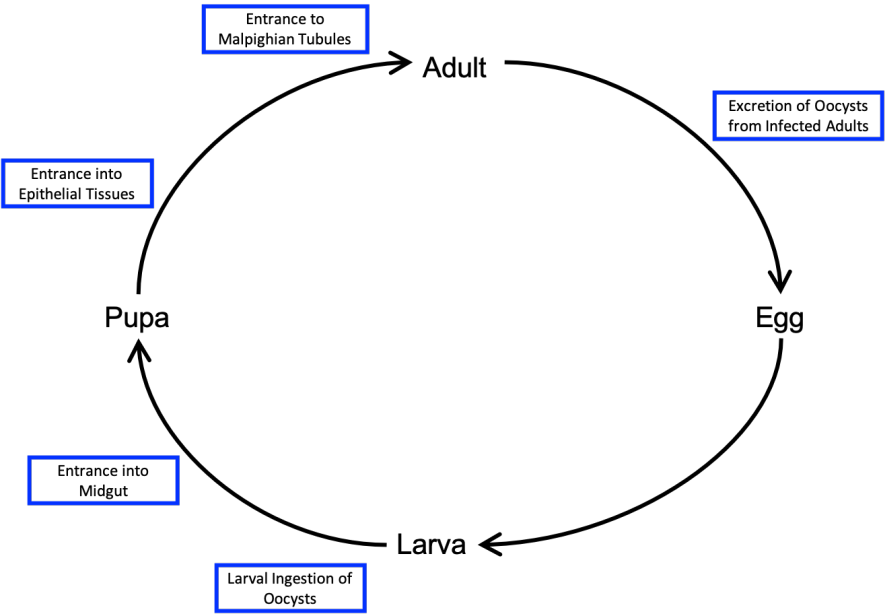
*Aedes albopictus* proportion

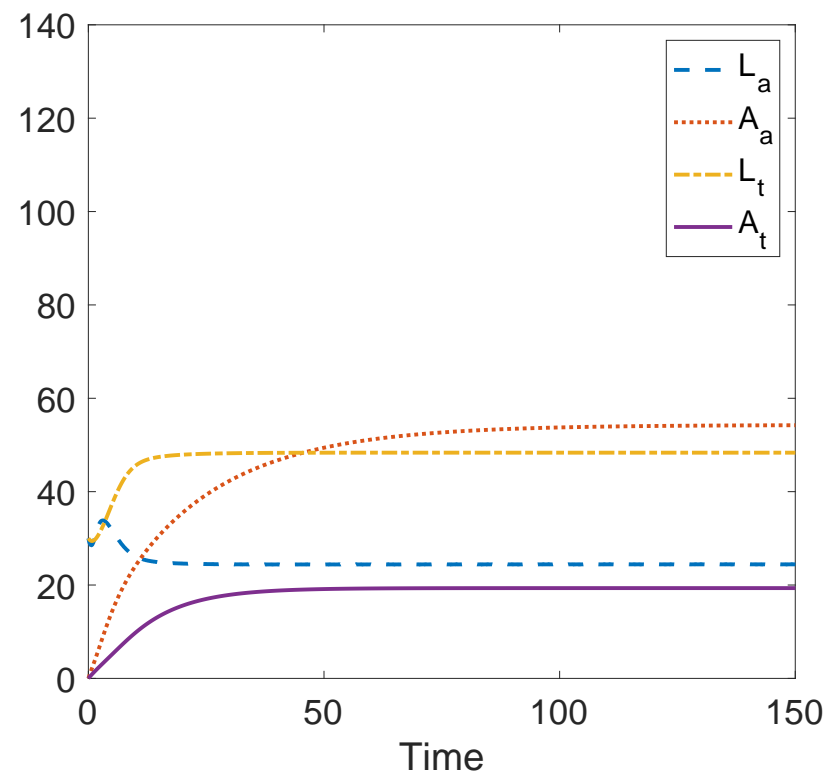
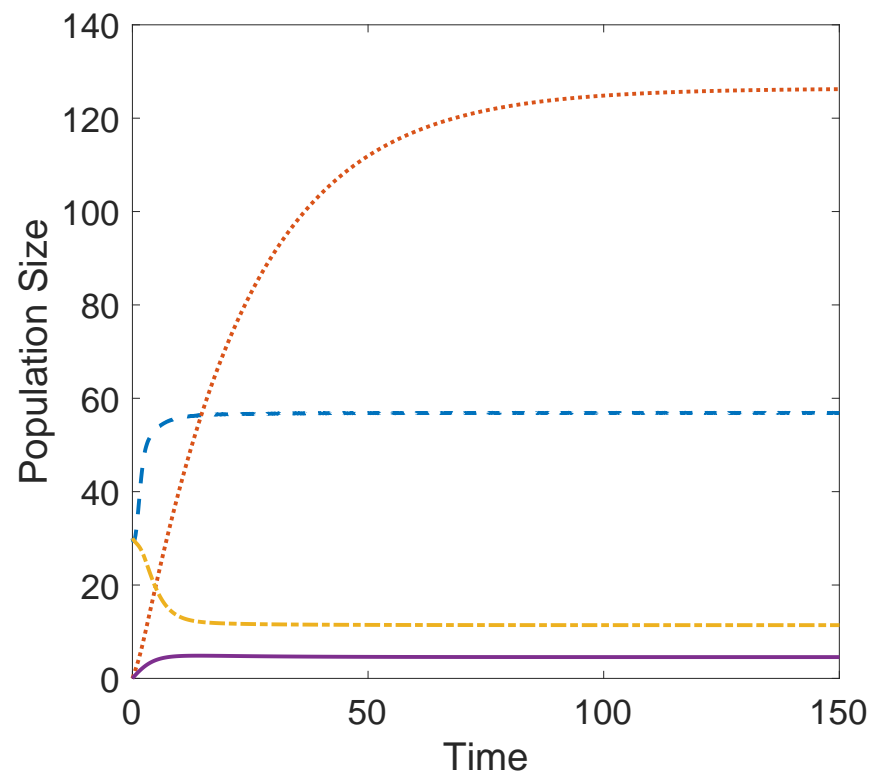
*Aedes triseriatus* proportion

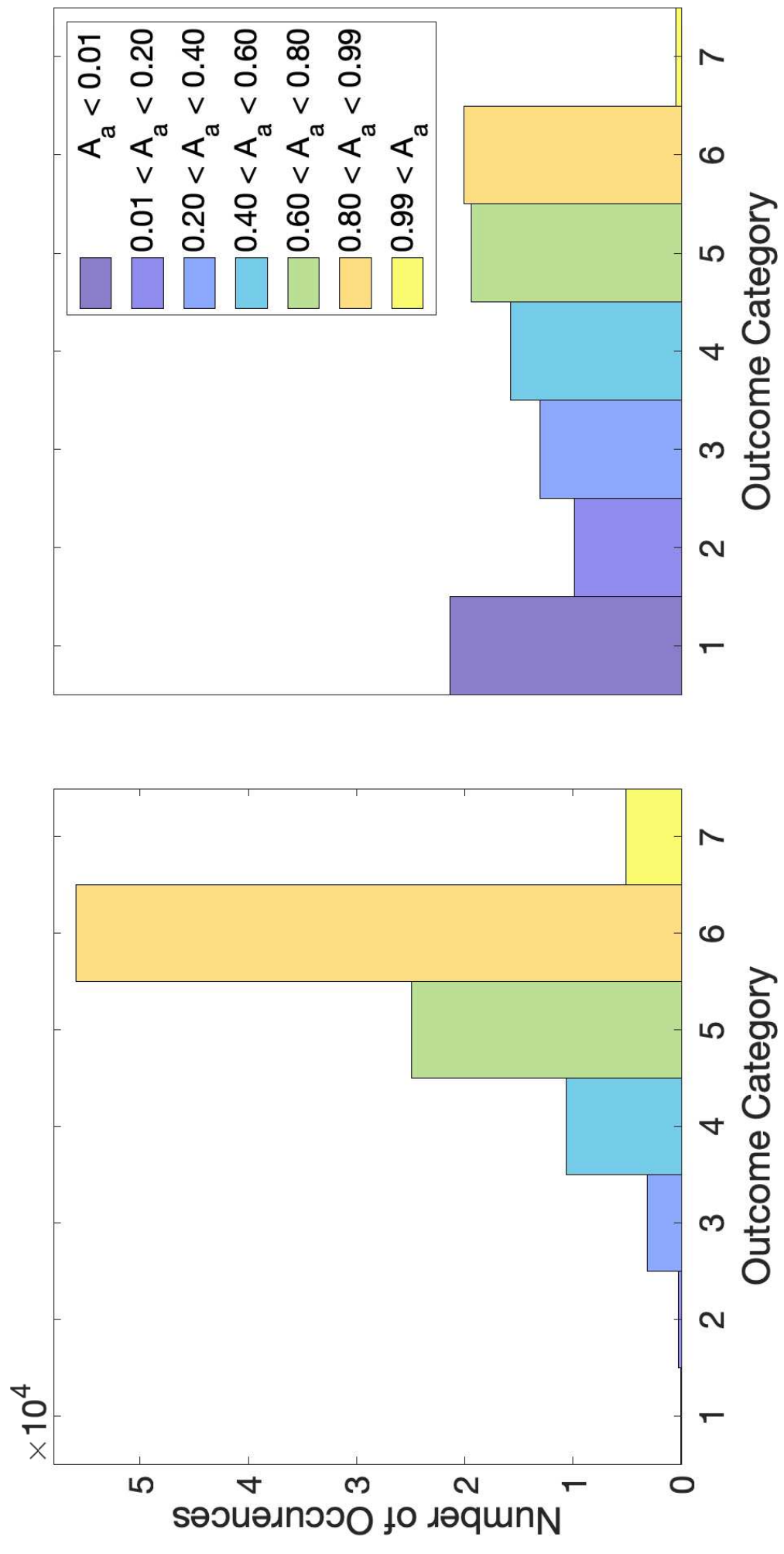
*Aedes albopictus* proportion

*Aedes triseriatus* proportion

Figure ***Aedes* mosquito Lifecycle with *Ascogregarina* infection**







Figure

