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Variability of Intra- and Interspecific Competitions of Bamboo Stump Mosquito Larvae over Small and Large Spatial Scales
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Source: *Oikos*, Vol. 97, No. 1 (Apr., 2002), pp. 87-96
Published by: Wiley on behalf of Nordic Society Oikos
Stable URL: https://www.jstor.org/stable/3547596
Accessed: 30-09-2021 15:14 UTC

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Sunahara, T. and Mogi, M. 2002. Variability of intra- and interspecific competitions of bamboo stump mosquito larvae over small and large spatial scales. – Oikos 97: 87–96.

We carried out field experiments to examine the variability of interspecific competition of mosquito larvae among microcosms in a bamboo grove (small spatial scale) and between bamboo groves at two sites, with single and multiple mosquito species (large spatial scale). Four types of microcosms that differed in capacity and litter input were set. In the hillside bamboo grove, where multiple species occurred, succession of the predominant species from *Aedes albopictus* to *Tripteroides bambusa* was observed in control microcosms from which no mosquito larvae were removed. Weekly removal of competitive species resulted in increased pupation of *A. albopictus* and adult body weight under both rich and poor resource conditions. In the late period of the experiments, the effect of competitor removal on pupation of *A. albopictus* was greater in deep containers that never dried than in shallow containers that were dried in the laboratory. The number of eggs showed a slight difference between competitor-excluded and deep control microcosms. These results indicate that interspecific competition limits pupation of *A. albopictus* more strongly in deep containers than in shallow and drought-prone containers.
Compared with the hillside site, the larval density of *A. albopictus* attained a higher density in the bamboo grove in the plain where no competitive species occurred, due to a higher oviposition rate. Lower rate of pupation and lower adult weight at the plain site than at the hillside site indicated that resource limitation was more severe at the plain site. Populations of *A. albopictus* at hillside and plain sites appeared to suffer from strong inter- and intraspecific competition, respectively. At the hillside site, the intensity of interspecific competition appeared to increase later in the breeding season, with a high larval density of *T. bambusa*. In contrast, at the plain site, intensity of intraspecific competition appeared to be reduced later in the breeding season with decreasing larval density of *A. albopictus*.

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Interspecific interactions potentially influence performance of populations. In patchy environments, the significance of interspecific interactions may differ from one patch to another, when biotic and abiotic habitat conditions of each patch affect the outcomes of interactions. Patchy habitats often show nested hierarchical structures, i.e. multiple patches form a superpatch over a larger spatial scale (Inouye 1999, Roslin 2000). In these cases, a study with a certain spatial scale might

not be sufficient to understand how interspecific interactions affect population performances.

This paper deals with intra- and interspecific competitions among larval mosquitoes in bamboo groves, focusing on the population performance of *Aedes albopictus* (Skuse). Water-filled bamboo stumps harbor communities of aquatic insects dominated by mosquito larvae (Kurihara 1983, Sota and Mogi 1996, Sunahara and Mogi 1997a, Sunahara et al. 1999). Stumps are

scattered as discrete patches within a bamboo grove. On a larger spatial scale, bamboo groves are also scattered patchily. In both small and large spatial scales, we can see the variation in the opportunity of interspecific competition among "patches".

Bamboo stumps vary in morphology, which results in variation in capability to hold water and trap leaf litter. In the previous study (Sunahara and Mogi 1997b), we found that *A. albopictus* could complete larval development earlier than its major competitor, *Tripteroides bambusa* (Yamada) and hence become superior in short-term competition of a single generation. However, in the later stage of long-term competition involving multiple overlapping cohorts under a limited food condition, *T. bambusa* survived and developed better than *A. albopictus*. Observation of the distribution of the two species in a bamboo grove indicated that *T. bambusa* was predominant in persistent habitats whereas *A. albopictus* could use drought-prone stumps more efficiently (Sunahara and Mogi 1997a). These studies suggested that the potential effects of interspecific competition on performance of *A. albopictus* larval populations are greater in persistent habitats than in drought-prone ones. Drought is a major disturbance for communities in small aquatic habitats (McLachlan and Cantrell 1980, Bradshaw and Holzapfel 1988, Jenkins et al. 1992, Fincke 1994, Sota et al. 1994, Warren and Spencer 1996, Schneider 1997, Sunahara and Mogi 1997a, Sunahara et al. 1999). Several experimental studies on interspecific competition of tree-hole mosquitoes have been done using microcosms (Livdahl 1984, Chambers 1985, Livdahl and Willey 1991, Juliano 1998). These studies manipulate initial densities and species compositions and prevent further colonization of mosquitoes. Such a method can be used to evaluate how the presence of other species affects the survival and development of mosquito larvae of a single generation. However, in the field, it is possible that interspecific competition affects both colonization and development of certain species, and affects the larvae of multiple generations in the long term. Experimental removal of competitors would be the most powerful method to examine these effects. Comparison of the responses to competitor removal among different types of containers would clarify the variability in the significance of competition among patches over a small spatial scale.

On a larger spatial scale, mosquito fauna differs among bamboo groves. A four-year survey on the distribution of *T. bambusa* among bamboo groves indicated that this species occurs around a hillside where bamboo groves are dense, but does not occur in isolated bamboo groves in a plain (Sunahara and Mogi 1998). *A. albopictus* occur widely from hillsides to plains, and is the only species in most bamboo groves in the plain surveyed (T. Sunahara, pers. obs.). Therefore, it is expected that *A. albopictus* suffer from interspecific competition in bamboo groves in the hillside but not in

those in the plain. Comparison of population performances between bamboo groves with and without competitors would clarify the variation in the significance of competition among patches over a large spatial scale.

The present study examines the significance of interspecific competition in *A. albopictus* populations using experimental microcosms that simulate bamboo stumps. We address the following questions: (1) how the intensity of interspecific competition differs among microcosms that vary in litter input and drought susceptibility within a bamboo grove, and (2) how the performance of *A. albopictus* populations differ between bamboo groves with and without competitive species.

Methods

Study sites

The field study was done in two bamboo groves (sites M and K) in and around Saga City (33N 121E) from July to October 1999. Site M is located on a hillside (altitude, approximately 50 m) where large areas are covered with orange orchards. Many bamboo groves are scattered around the hillside. Site K is located within a plain that includes human population. Usually in this region, June and July are the months with high precipitation, however in 1999 much rainfall was also observed in August and September. Temperature and humidity conditions do not differ greatly between bamboo groves in the hillside and those in the plain (K. Ishizaka, pers. comm.). Preliminary surveys in 1994 and 1995 indicated that *A. albopictus* occurred widely in most of bamboo groves in the plain and the hillside including sites M and K, whereas distribution of other container-breeding mosquitoes were mostly limited to hillside areas. A detailed survey on distribution of *T. bambusa* indicated that this species rarely colonized bamboo groves which were isolated within a scale of several hundreds meters (Sunahara and Mogi 1998). Therefore, sites M and K represented the bamboo groves with multiple mosquito species and those occupied by *A. albopictus*, respectively.

Experimental design

On July 5, we set plastic cups (bottom and top diameter, 7 cm and 9 cm; height, 10 cm) in the bamboo groves. In each cup, a cork sheet of 3 × 10 cm area and 2 mm in thickness was attached with a metal clip as an oviposition substrate. At site M, 8 types of microcosms with 2 × 2 × 2 factorial design of resource, capacity, and exclusion of competitors were established with six replicates. Dead bamboo leaves, which had been collected at site M prior to the experiment, dried at room temperature and then kept in a desiccator, were initially

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introduced to microcosms, and then supplemented weekly. Leaves were cut into pieces of 2–3 cm long using scissors. For the "litter rich" class, the initial dry weight was 600 mg and then 60 mg was added every week. For the "litter poor" class, 300 mg was used for the initial condition, and 30 mg for the weekly addition. Under natural conditions, bamboo leaves fall mainly in April and May, and, after that period, leaf fall continues at a low level (Sunahara and Mogi 1997a). The number of leaves trapped varies greatly among bamboo stumps depending on the opened area of the stump (Sunahara and Mogi 1997a). The amounts of leaves per bottom area of the containers for the rich and poor conditions in the present study were within the range that was observed in the field. Leaves that naturally fell into microcosms were removed daily.

To make two classes of container capacity, we made a hole of approximately 5 mm in diameter in the sides of the cups so that they could hold 300 ml (depth, 7.5 cm) or 150 ml (depth, 4 cm) of water as the maximum volume. At the beginning of the experiment, the microcosms were filled with distilled water. Hereafter, the two capacity classes will be noted as "deep" and "shallow" microcosms, respectively.

Once a week (Monday), we collected the microcosms from the field. They were kept separately in sealed plastic bags, and transferred to the laboratory. Larvae were sorted to species or genus (larvae of *A. albopictus* and *Aedes flavopictus* Yamada could not be distinguished), and counted for each developmental stage (1st–4th instars and pupa). Mosquito larvae of *Aedes* spp. were returned to the microcosms but other larvae were removed from the microcosms of treatment "excluded". All mosquito larvae from control microcosms were returned to the original microcosms. Microcosms were returned to the field on the next day (Tuesday).

At site K where only *A. albopictus* occurred, 4 types of microcosms (2 × 2 factorial design of resource and capacity with the same conditions as site M) were set. For each treatment, six replicates were made. The microcosms were collected from the field on Monday, and were returned on the next day after counting *A. albopictus* larvae and pupae. One deep litter-poor microcosm at site K was excluded from analysis because it received bird droppings and many adult mosquitoes emerged from it.

Microcosms were checked daily in situ, and pupae, if any, were collected and brought to the laboratory. By the daily census, we could basically collect all mosquito pupae that emerged from each microcosm during the course of the experiment. Pupae from each microcosm were reared to adult in a plastic tube covered with a mesh sheet in the laboratory. Adults were killed with chloroform, then identified to species, sexed and weighed to the nearest 0.01 mg by a semi-micro balance (BP 210 D, Sartorius, Tokyo) immediately after they were killed. Pupae that died during rearing in the

laboratory were identified to species or genus (pupae of *A. albopictus* and *A. flavopictus* could not be distinguished). Dead pupae of *Aedes* spp. were counted as those of *A. albopictus* since the majority of emerged adults were this species (see Results).

During the course of the experiment, we changed two aspects of the experimental setting. First, we changed the color of the cups. By late July, it became explicit that the microcosms set in the bamboo groves were unfavorable for *T. bambusa*, a predominant species at site M, for colonization possibly because of their white color. We observed that *T. bambusa* larvae were abundant in bamboo stumps, the outer walls of which were dark, but only a few *T. bambusa* larvae were found in the microcosms we set. Therefore, on August 5, we covered the sides and tops of all cups with black vinyl, with an opening of 10 cm diameter at the top, in an attempt to enhance the colonization of *T. bambusa* to similar levels as the bamboo stumps. Second, we manipulated the drought. In the beginning of the experiment, we hoped that the shallow microcosms would dry up at a higher frequency than the deep ones. However, because of abundant rainfall in the summer of 1999, none of the microcosms dried during 8 weeks from the beginning of the experiment. On August 30, we brought all microcosms to the laboratory, and dried them in a room with a dehumidifier and a fan. One week later, all of the shallow cups and none of the deep cups were dried. We filled each microcosm with distilled water to the maximum volume and returned them to the field on September 7. We continued the experiment until October 2. The experimental period was divided into 3 periods as follows: period 1, weeks 0–4 (cups were not covered with black sheets); period 2, weeks 5–9 (until shallow microcosms were dried in laboratory); period 3, weeks 10–13 (after the drought).

At the end of periods 1, 2 and 3, the number of eggs on the cork sheet was counted for each microcosm under a stereomicroscope. The eggs laid on the cork sheet included those of genera *Aedes*, *Armigeres*, *Ochlerotatus* and *Tripteroides*. Eggs of *Tripteroides* were distinguishable from others, but we could not separate species of the other genera at the egg stage. Therefore, the data represent the total number of eggs of genera *Aedes*, *Armigeres* and *Ochlerotatus* at site M. At the end of period 1, the cork sheet was replaced. Each collected sheet was kept in a glass tube for 1 week with the same water level as the microcosm from which the sheet was collected. Larvae hatched in this period were introduced to the original microcosms. The numbers of hatched and unhatched eggs were counted for each microcosm after these larvae hatched. At the end of period 2, the cork sheets were not replaced. The number of eggs was counted the day after microcosms were brought to laboratory (September 1), then the cork sheet was returned to the original microcosms. Also at the end of period 3, the number of eggs on the cork sheets was counted directly after they were collected.

Results

Microcosm types and interspecific competition at site M

At site M, the four types of control (competitors not excluded) microcosms were colonized by five mosquito species: *A. albopictus*, *A. flavopictus*, *Ochlerotatus japonicus* (Theobald), *Armigeres subalbatus* (Coquilett), and *T. bambusa*. Of these, *A. albopictus* and *T. bambusa* were abundant and the others occurred infrequently (Fig. 1). The numbers of adults identified as *A. albopictus* and *A. flavopictus* from all the microcosms at site M were 1848 and 13, respectively. Therefore, most *Aedes* spp. larvae can be considered as *A. albopictus*.

In period 1, *Aedes* spp. were the primal occupants of each type of control microcosms, however *T. bambusa*

larvae became abundant after microcosms were covered with black sheets in period 2 (Fig. 1). In period 3, *T. bambusa* became more abundant than *Aedes* spp. in deep control microcosms, however that was not the case for shallow control microcosms that dried in week 9 (Fig. 1).

Weekly removal of larvae of competitive species effectively reduced the density of old-stage larvae of *T. bambusa*, the predominant competitor (Fig. 1). Although we failed to remove all larvae of species other than *A. albopictus* before pupation, the numbers of pupae of these species collected from competitor-excluded microcosms were small (in total, 5 *A. flavopictus* and 8 *O. japonicus* from 4 types of competitor-excluded microcosms). We consider that our treatment successfully reduced the intensity of interspecific competition.
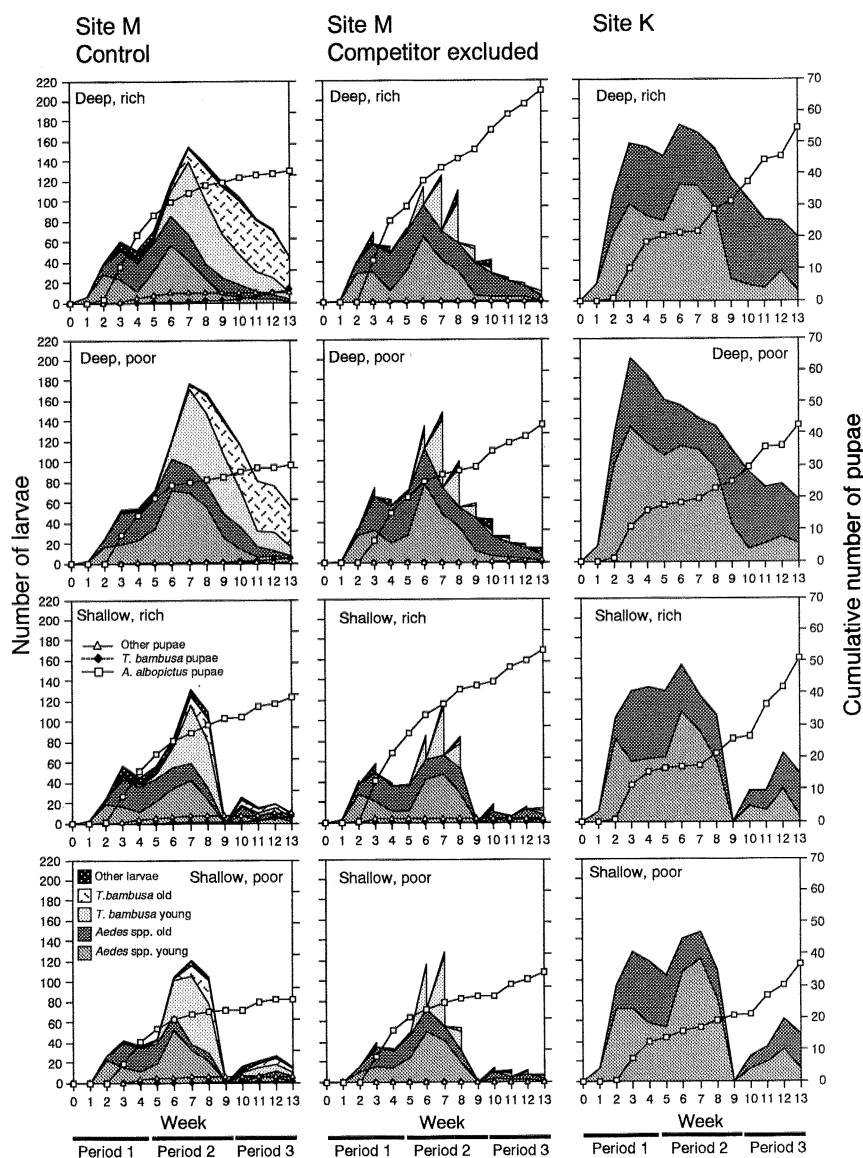

Fig. 1. Change in the number of larvae and cumulative number of pupae of each mosquito species in the microcosms at sites M and K. Young and old stages indicate instars 1 + 2 and 3 + 4, respectively. Other larvae and pupae include *O. japonicus* and *Ar. subalbatus*.
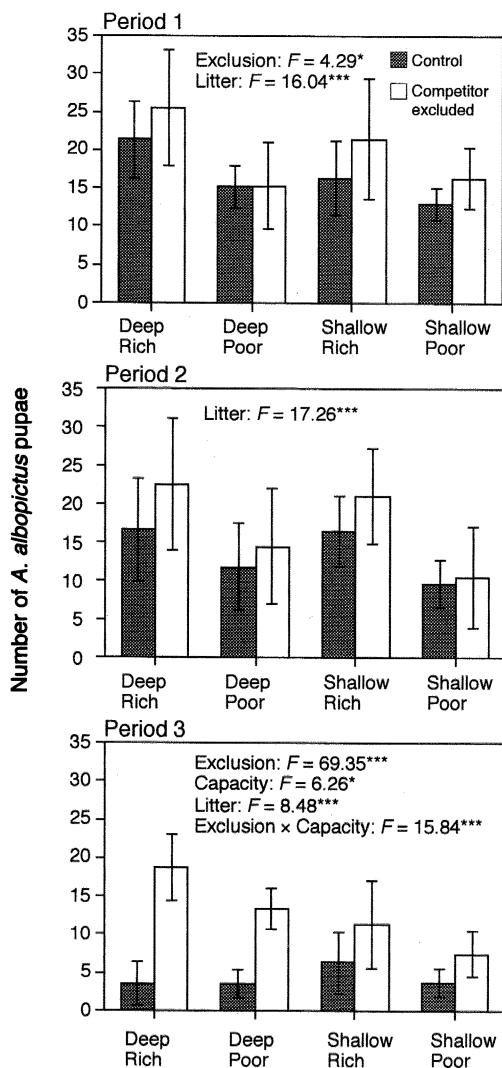
Fig. 2. Comparison of the number of *A. albopictus* pupae (mean ± SD) between control and competitor-excluded microcosms at site M. Significant effects in 3-way ANOVA are given in the figures.

Larval densities of *Aedes* spp. in competitor-excluded microcosms did not differ significantly from those in control microcosms (Fig. 1; ANOVA with 3 factors, exclusion, capacity and litter, for the cumulative larval count; F values for exclusion: $F = 0.020$, $F = 0.335$, and $F = 0.070$ for periods 1, 2, and 3, respectively, $P > 0.05$ for each period).

Significant effects of competitor-exclusion on the number of pupae were detected in periods 1 and 3 (Fig. 2). In period 3, the difference in the number of pupae between control and competitor-excluded microcosms was greater in deep microcosms (mean: 3.5 and 16.0, respectively, rich and poor combined) than in shallow ones (5.0 and 9.4, respectively), which resulted in a significant interaction of exclusion and capacity (Fig.

2). In all periods, the amount of litter had a significant effect on the number of *A. albopictus* pupae (Fig. 2).

Both male and female adult weights were largest in period 1 and became smaller in period 2 (Fig. 3). Adult weights increased in shallow microcosms and competitor-excluded deep microcosms in period 3, however those in deep control microcosms remained at low levels (Fig. 3). In period 3, the effects of exclusion and capacity on adult weight were significant in both males and females (Fig. 3).

The numbers of eggs on cork sheets are shown in Table 1. As these eggs did not include *T. bambusa* eggs,
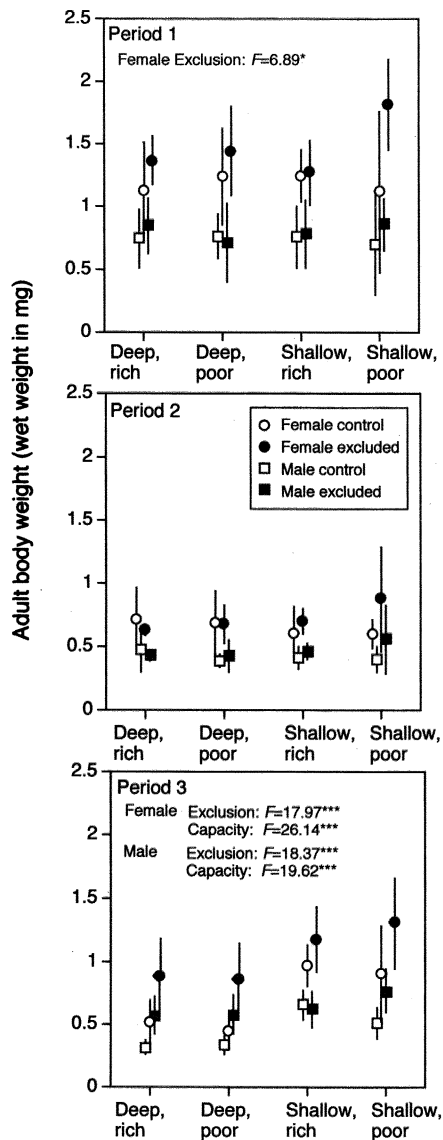

Fig. 3. Comparison of the average male and female weight of *A. albopictus* adults (mean ± SD) emerged from control and competitor-excluded microcosms at site M. Significant effects in 3-way ANOVA are given in the figures. ANOVA for period 2 was not done because variance for both sexes was not homogeneous.

Table 1. Mean and SD of the number of eggs in each type of microcosms at sites M and K. Percentage of hatched eggs is given in parentheses.

Capacity	Litter	Site	Competitor exclusion	Number of eggs (% hatched)		
				Period 1[a]	Period 2 [a]	Period 3
Deep	Rich	site M	Control	74.7 ± 23.3 (83.9%)	105.3 ± 24.5 (81.3%)	70.8 ± 32.7 (80.7%)
			Excluded	84.2 ± 36.8 (93.7%)	136.2 ± 41.7 (79.2%)	113.2 ± 24.3 (82.8%)
		site K	–	104.8 ± 35.7 (93.5%)	124.0 ± 55.3 (80.2%)	195.7 ± 113.7 (54.2%)
	Poor	site M	Control	46.3 ± 23.5 (92.8%)	86.2 ± 19.0 (84.7%)	64.0 ± 30.1 (75.3%)
			Excluded	74.2 ± 37.5 (86.7%)	141.0 ± 47.4 (81.7%)	89.8 ± 28.7 (89.2%)
		site K	–	145.2 ± 50.0 (96.4%)	109.4 ± 30.2 (82.6%)	265.0 ± 129.3 (46.3%)
Shallow	Rich	site M	Control	57.5 ± 46.3 (95.4%)	107.5 ± 30.3 (77.5%)	97.0 ± 42.0 (77.3%)
			Excluded	54.0 ± 31.8 (93.2%)	95.3 ± 29.3 (82.5%)	85.8 ± 21.5 (65.2%)
		site K	–	83.8 ± 18.8 (93.8%)	175.5 ± 42.8 (76.3%)	347.3 ± 147.9 (56.0%)
	Poor	site M	Control	25.5 ± 19.4 (94.8%)	109.3 ± 54.0 (80.8%)	84.5 ± 51.1 (85.4%)
			Excluded	16.3 ± 9.7 (87.8%)	81.7 ± 37.5 (77.8%)	78.8 ± 28.1 (59.6%)
		site K	–	70.8 ± 21.8 (94.4%)	168.8 ± 46.8 (75.4%)	280.0 ± 91.4 (54.9%)

[a] Substrates were replaced after period 1, but were not after period 2.

and as *A. flavopictus*, *O. japonicus* and *Ar. subalbatus* occurred infrequently (Fig. 1), most of the eggs at site M can be considered as *A. albopictus* eggs. During period 1, more eggs had been laid in deep microcosms than in shallow ones at site M (ANOVA with 3 factors, capacity, litter and exclusion, log $(X + 1)$ transformed; F for capacity, $F = 22.03$, $P < 0.001$), and in litter-rich ones than in litter-poor ones (F for litter, $F = 14.16$, $P < 0.01$). At the end of periods 2 and 3, significant interaction of exclusion and capacity was detected for microcosms at site M, i.e. the number of eggs was larger in competitor-excluded than in controls in deep microcosms, however the number of eggs was slightly larger in the control in shallow microcosms (Table 1; ANOVA, F for capacity × litter, $F = 8.56$ and $F = 4,81$ for periods 2 and 3, respectively, $P < 0.01$ for both periods). The percentage of hatched eggs was generally high in each type of microcosm and in each period at site M, showing no apparent patterns related to treatment (Table 1).

Comparison of the two sites

Hereafter we compare the performance of *A. albopictus* between control microcosms at site M and microcosms at site K. Compared to the larval density of *Aedes* spp. at site M, that of *A. albopictus* at site K was high throughout the experimental periods (Fig. 1; ANOVA with 3 factors, site, capacity and litter, for the cumulative larval count; F values for site: $F = 164.7$, $F = 169.8$, and $F = 174.0$ for periods 1, 2, and 3, respectively, $P < 0.001$ for each period).

The number of *A. albopictus* pupae was smaller at site K than at site M in periods 1 and 2, although the site effect was not significant by ANOVA for period 1 (Fig. 4). In period 3, the number of pupae was significantly larger at site K than at site M in every type of

microcosms (Fig. 4). Adult weights of both males and females were significantly smaller at site K than at site M in period 1, and the difference was significant for males in period 2 (Fig. 5). In period 3, adult weight did not differ significantly between the two sites. Shallow microcosms produced heavier adult males and females at both sites in period 3.

The number of eggs was larger at site K than at site M during the whole period (Table 1; ANOVA with 3 factors, site, capacity and litter, log $(X + 1)$ transformed for period 3, F for site, $F = 29.81$, $F = 13.00$ and $F = 71.58$ for periods 1, 2 and 3 respectively, $P < 0.001$ for each period). The difference between the two sites was especially great in period 3. At the end of period 3, the percentage of hatched eggs was low at site K (Table 1).

Discussion

Variability within a bamboo grove

In the control deep microcosms at site M, the predominant species shifted from *A. albopictus* to *T. bambusa*. The succession of the two species is consistent with a previous laboratory experiment (Sunahara and Mogi 1997b) and field observation (Sunahara and Mogi 1997a). Since *T. bambusa* appeared to avoid the white color of the cups, the predominance of *A. albopictus* in period 1 should be considered as an artifact. We can conclude at least that even when the microcosms were predominated by *A. albopictus* artificially in the early stage, *T. bambusa* could take over in the late stage. Exclusion of competitors clearly increased pupal production of *A. albopictus* in period 3. This is direct evidence for the fact that the presence of competitive species, especially *T. bambusa*, suppressed production of *A. albopictus* in the field. At site M, a significant effect of litter on the number of pupae was observed

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throughout the experimental period. Adult body weight was smaller in control microcosms than in competitor-excluded ones in period 3. These results suggest that interspecific competition for food resources reduced pupal production of *A. albopictus*.

The presence of competitors might also affect colonization. In periods 2 and 3, the number of eggs was larger in competitor-excluded deep microcosms than in control ones, suggesting oviposition-site preference by adult *A. albopictus* females. It has been reported that gravid females of *Aedes triseriatus* responded to the larval density (Edgerly et al. 1998). The smaller number of eggs in control than in competitor-excluded micro-
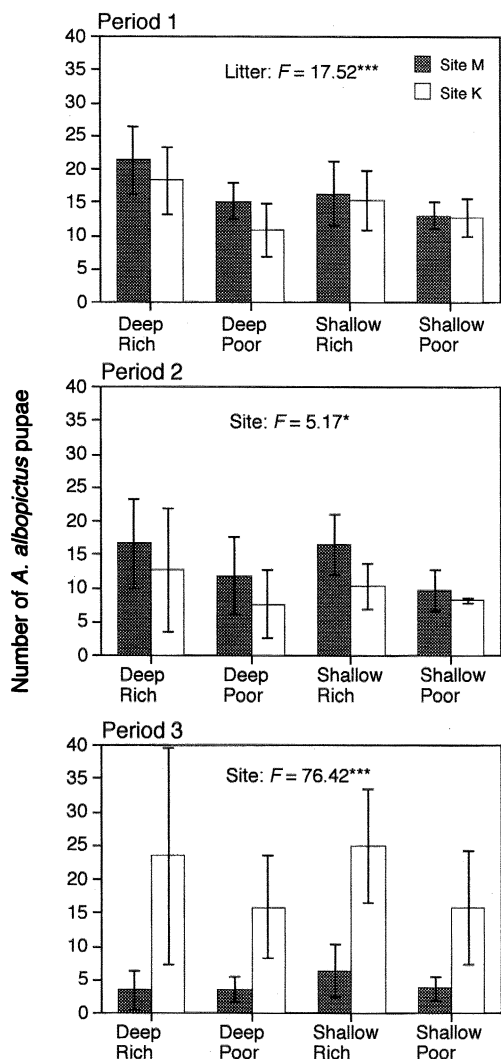

Fig. 4. Comparison of the number of *A. albopictus* pupae (mean ± SD) between control microcosms in site M and those in site K. Significant effects in 3-way ANOVA are given in the figures. For period 2, 3-way ANOVA was not done because variance was not homogeneous. Instead, ANOVA with 2 factors, sites and capacity, was done. Data for period 3 was log (X + 1) transformed prior to the analysis to homogenize the variance.
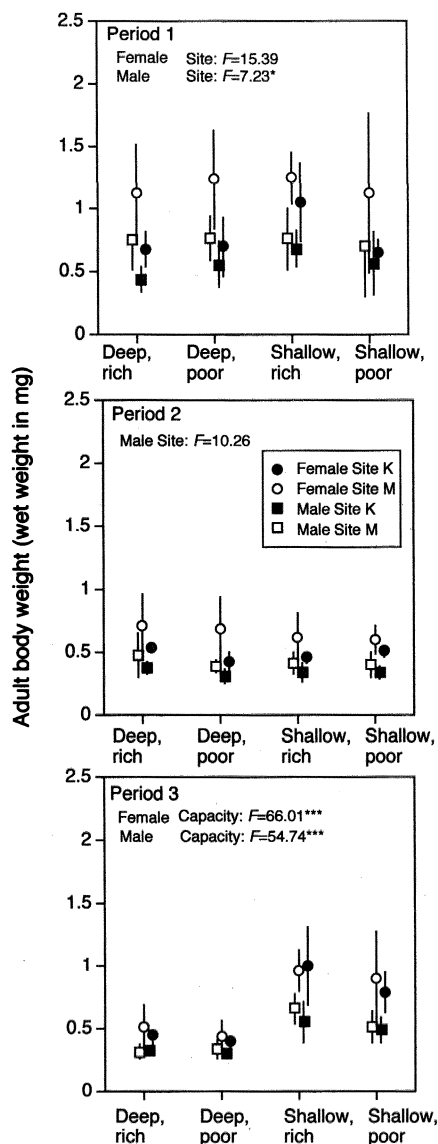

Fig. 5. Comparison of the average male and female weight of *A. albopictus* adults (mean ± SD) emerged from control microcosms at site M and those at site K. Significant effects in 3-way ANOVA are given in the figures. Only males were analyzed in period 2 because variance for female was not homogeneous.

cosms might be due to the higher larval density in control microcosms. In addition, a higher oviposition rate was observed in shallow microcosms than in deep ones in period 3 at site K, which also suggested that gravid females might avoid microcosms with high larval densities. In period 3, competitor-excluded deep microcosms at site M produced more than 4 times the number of *A. albopictus* pupae than did controls. The difference in the number of eggs between competitor-excluded and control deep microcosms was less than 2-fold in any period. Therefore, smaller pupal produc-

tion of *A. albopictus* in the presence of competitive species should be mainly due to decreased survival and development rates, rather than decreased colonization rate.

In period 3, a significant interaction was detected between effects of capacity and competitor-exclusion, indicating that the effect of interspecific competition was stronger in deep microcosms than in shallow ones. This must be due to drought at shallow microcosms in the end of period 2. After the drought, the larval density of *T. bambusa* in shallow microcosms did not recover quickly, resulting in a smaller difference in pupal production of *A. albopictus* between control and competitor-excluded microcosms compared with deep microcosms. It has been reported that drought affect the community structure of mosquitoes (Bradshaw and Holzapfel 1988, Jenkins et al. 1992, Sota et al. 1994, Sunahara et al. 1999) and other organisms in small aquatic sites (McLachlan and Cantrell 1980, Fincke 1994, Warren and Spencer 1996, Schneider 1997). In these systems, drought-resistant species are often specialized to drought-prone habitats where predation and competition are not severe (Bradshaw and Holzapfel 1988, Fincke 1994). For *A. albopictus*, which has high desiccation resistance in egg stage (Sota and Mogi 1992) and can complete larval development in a short time under favorable conditions (Sunahara and Mogi 1997b), drought-prone containers may be refuges from competitive species.

Competition for resource might be alleviated by a large amount of resource input. A positive relationship between productivity and species diversity was reported for tree-hole communities (Srivastava and Lawton 1998). In the present study, a significant effect of litter on pupation of *A. albopictus* was detected, which confirmed the importance of litter as a limiting factor of mosquito production, as reported by several authors for tree hole mosquitoes (Carpenter 1982, 1983, Léonard and Juliano 1995, Yanoviak 1999, Maciá and Bradshaw 2000). However, we found no evidence that interspecific competition was less severe in litter-rich microcosms. It appeared that in both litter-rich and poor microcosms, the larval density of *T. bambusa* attained a high enough level to inhibit development of *A. albopictus*. In containers that hold water persistently, larval density of *T. bambusa* can become high, since delayed larval development results in accumulation of several cohorts. In such a situation, the amount resource might not be important in determining the outcome of interspecific competition, at least within the range of resource conditions employed in our experiment.

To summarize, *T. bambusa* eventually predominated the containers and suppressed pupal production of *A. albopictus*, and this effect was alleviated by drought. Thus, the intensity of interspecific competition varied among containers within a bamboo grove, depending on the drought susceptibility of the containers.

Variability among bamboo groves

Compared with site M, a higher larval density of *A. albopictus* was observed at site K throughout the experimental period. The higher larval density was attributed a higher oviposition rate. It is unclear whether the higher oviposition rate of *A. albopictus* at site M compared to site K was due to the absence of the competitive species or different environmental conditions that limit adult survivorship and fecundity, such as availability of blood source. *A. albopictus* bites humans aggressively. Tsuda et al. (1994) reported that *A. albopictus* occurred more frequently in tree holes near human-populated areas than those deep in the mountains. It is possible that a human population near the bamboo grove in site K partly supported a high density *A. albopictus* population.

The higher larval density at site K, however, did not result in a greater number of pupae in periods 1 and 2. A smaller number of pupae and lighter adult weight in site K during periods 1 and 2 suggested that the effect of intraspecific competition of *A. albopictus* at site K was more severe than the combined effects of intra- and interspecific competition at site M. The absence of the competitive species appeared not to result in a greater production of mosquitoes in the peak population period. However, greater pupal production might be realized with a moderate larval density. In period 3, greater pupal production of *A. albopictus* was observed at site K than at site M. These results suggest that the difference in the effects of intra- and interspecific competition on mosquito production depends on the phenology of the species. Larvae of *A. albopictus* are mainly found from May to October, showing a population peak in August (Mori 1979, Sunahara and Mogi 1997a), while the larval density of *T. bambusa*, which overwinters both as an egg and a larva, becomes high in bamboo stumps with persistent water later in the breeding season (Sunahara and Mogi 1997a, c). *A. albopictus* overwinters as a dormant egg that is laid from mid-September in this region (Mori et al. 1981). The strong interspecific competition later in the breeding season at site M might result in a small overwintering-population size of *A. albopictus*, as suggested by the small number of eggs and the high percentage of hatched eggs in period 3 at site M, which would determine the abundance of *A. albopictus* early in the next breeding season.

Coupling small and large scales

The present study showed that the variations in intensity of intra- and interspecific competitions are observed both in small and large spatial scales. Coupling scopes of large and small spatial scales would help us to understand the relationship between local and regional processes in community organization.

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As noted above, *A. albopictus* is superior to *T. bambusa* in colonizing drought-prone containers. The difference in colonizing ability between the two predominant mosquitoes may explain not only their local coexistence in hillside bamboo groves but also their distribution patterns over a larger spatial scale. *A. albopictus* can use various types of drought-prone small containers in open areas as larval habitats whereas *T. bambusa* rarely occurs in open areas (Sunahara et al. 2002). It is possible that *A. albopictus* can colonize isolated bamboo groves by using these temporary habitats as stepping stones. This situation resembles the case of coexistence of a superior competitor but poor colonizer and an inferior competitor but superior colonizer which has been studied both empirically (Paine 1979, Hanski and Ranta 1983, Tilman 1990) and theoretically (Hanski 1983, Nee and May 1992). On a larger spatial scale, bamboo groves in a plain such as site K appear to be refuges for *A. albopictus* from competitive species. An interesting subject for future study would be to investigate whether specialization in use of certain kinds of containers (e.g. drought-prone ones) by *A. albopictus* differs among sites with or without competitors.

In addition, from the present study we may predict possible effects of large-scale habitat degradation on local populations of *A. albopictus*, the nuisance mosquito. *T. bambusa* does not occur in isolated bamboo groves on plains (Sunahara and Mogi 1998). The reduction and isolation of bamboo groves may result in extinction of local populations of *T. bambusa* and reduction of intensity of interspecific competition in relatively persistent aquatic sites in deep bamboo stumps. Production of *A. albopictus* from these stumps may not increase greatly during the period of peak population, due to severe intraspecific competition, however production of this mosquito would increase later in the breeding season with a moderate larval density.

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