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Drought and overwintering success of *Tripteroides bambusa* (Diptera: Culicidae) larvae and eggs in a bamboo grove

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Abstract: We studied the effects of winter drought on the overwintering success of larvae and eggs of *Tripteroides bambusa* in a bamboo grove in northern Kyushu, southwestern Japan. A half of the bamboo stumps which harbored the 3rd and 4th instar larvae of *T. bambusa* in November 1995 dried up at least once in winter and almost all the larvae in them died. From November 1995 to March 1996, the total number of overwintering 3rd and 4th instar larvae in the study area decreased from 1208 to 225. The incidence of *T. bambusa* larvae increased from March, when the new cohort from overwintering eggs appeared and the total number of 2nd-4th instar larvae and pupae reached 2994 in May. About a half of them existed in stumps which had dried up at least once in winter, indicating that the overwintering eggs of *T. bambusa* have desiccation resistance. In spring, *T. bambusa* became abundant earlier than did other mosquitoes such as *Aedes albopictus* and *A. japonicus*, and could grow without the major competitors. These overwintering characteristics of *T. bambusa* can facilitate its predominance in the bamboo grove.

INTRODUCTION

Winter is a severe season for mosquitoes in temperate regions. To survive winter, they have diapause stages in their life cycles. Success or failure in overwintering should strongly affect the initial population size in the following breeding season, and hence, subsequent population growth. Thus, the availability of favorable overwintering sites may be one of the important factors that limit the distribution and abundance of mosquito populations.

In bamboo groves in Kyushu, southwestern Japan, several mosquitoes use the water-filled bamboo stumps as larval habitats and overwinter there as diapause eggs or larvae. The bamboo stumps differ from each other in size and structure and,

consequently, in the capacity to keep water and receive nutrient resources such as fallen leaves (Sota *et al.*, 1994; Sota 1996; Sunahara and Mogi submitted). How do the bamboo stump characteristics affect the overwintering success of mosquitoes?

This paper focuses on the overwintering of *Tripteroides bambusa* (Yamada), one of the common mosquitoes in bamboo stumps as well as tree holes in this region (Sota *et al.*, 1994; Tsuda *et al.*, 1994). This mosquito overwinters as either larva or egg (Makiya, 1968; Mori *et al.*, 1985; Mogi, 1995). In this paper, we examine the effect of winter drought on the overwintering success of larvae and eggs of *T. bambusa* in bamboo stumps. In addition, by comparing overwintering of *T. bambusa* with that of *Aedes albopictus* (Skuse) and *A.*

japonicus (Theobald), which are the potential competitors of *T. bambusa* and are the nuisance mosquitoes in this region, we discuss the significance of the overwintering process in organization of the mosquito community in a bamboo grove.

MATERIALS AND METHODS

This study was carried out in a bamboo (*Phyllostachys heterocycla* f. *pubescens* Muroi) grove in Mikazuki Town, Saga Prefecture (33°18' N, 130°13' E). Climate and weather conditions of the area were described in Sunahara and Mogi (submitted). Briefly, there was much rainfall in spring to summer and little in autumn and winter in the study period. Six mosquitoes were observed in this bamboo grove: *T. bambusa*, *A. albopictus*, *A. japonicus*, *Culex kyotoensis* Yamaguti et LaCasse, *Uranotaenia novobscura* Barraud and *Topomyia yanbarensis* Miyagi, from the most frequent. The distribution patterns of the predominant larval mosquitoes among bamboo stumps in this grove are reported elsewhere (Sunahara and Mogi, submitted).

We carried out monthly census within an area of 35 m × 25 m inside the bamboo grove from July 1995 to June 1996, except for January 1996. We labeled the bamboo stumps when they were found with water inside for the first time. In this paper, we use the data of 64 stumps that were labeled by November 1995. The number of fallen leaves trapped in the stump was counted and marked by cutting their petioles in each census. If water existed in the stump, all the water in the stump was drained by siphoning or pipetting into white plastic pans to examine the densities of mosquito immatures. The presence or absence of each developmental stage of *T. bambusa* immatures and 2nd–4th instar larvae of *A. albopictus* and *A. japonicus* was recorded. After examining the presence or absence of larval mosquitoes, all water, leaf litter, and the inhabitants were returned to the stump. The number of the

Table 1. Categorization of bamboo stumps with regard to persistence of water during winter 1995–1996.

Category	Presence/absence of water			No. of stumps
	Nov	Dec	Feb	
Group A	+	+	+	12
Group B	+	–	+	8
Group C	+	–	–	8
	–	–	+	
Group D	–	–	–	36

3rd and 4th instar larvae of the mosquitoes was counted from November 1995. From April 1996, we also counted the number of the 2nd instar larvae (3 species) and pupae (only *T. bambusa*). We considered that *T. bambusa* larvae hatched from overwintering eggs were present in a bamboo stump, (1) if the 1st or 2nd instar larvae of *T. bambusa* were found in March or April 1996 in a stump where neither of them were found in the previous census, or (2) if more than 30 1st or 2nd instar larvae were found in a stump in March or April (the number of the overwintering 1st and 2nd instar larvae was below this level, if any).

To examine the effect of drought on the overwintering of *T. bambusa* immatures, we categorized the stumps into 4 groups, with regard to the water persistence in winter (Table 1). For the analysis of the effect of the leaf input on the number of larvae and pupae, we used data from April to May or June 1996, because the amount of fallen bamboo leaves increased from April.

RESULTS

The number of water-filled bamboo stumps was large in summer (Table 2). Major droughts in mid September and December caused drastic decreases in the number of stumps with water. *Tripteroides bambusa* larvae was most abundant in August. The incidence (proportion of stumps with larvae) of *T. bambusa* kept at high levels until December, then decreas-

Table 2. Seasonal trends in occurrence of the three mosquito immatures in bamboo stumps.

Census	Date	Number of stumps with water	Number (proportion) of stumps with mosquito immatures						
			<i>Tripteroides bambusa</i>			<i>Aedes albopictus</i>		<i>Aedes japonicus</i>	
			Instar I-II	Instar III-IV	Pupae	Instar II	Instar III-IV	Instar II	Instar III-IV
1995									
July	18-24	49	11 (0.22)	27 (0.55)	18 (0.37)	NR	32 (0.65)	NR	17 (0.35)
Aug	17-19	45	27 (0.60)	39 (0.87)	13 (0.29)	NR	42 (0.93)	NR	8 (0.18)
Sept	19-21	21	18 (0.86)	21 (1.00)	12 (0.57)	NR	13 (0.62)	NR	1 (0.05)
Oct	19-23	21	16 (0.76)	20 (0.95)	1 (0.05)	NR	3 (0.14)	NR	0 (0.00)
Nov	22-27	26	16 (0.62)	20 (0.77)	0 (0.00)	NR	1 (0.04)	NR	1 (0.04)
Dec	20-21	12	9 (0.75)	10 (0.83)	0 (0.00)	NR	0 (0.00)	NR	0 (0.00)
1996									
Feb	14-16	22	5 (0.23)	10 (0.45)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)	0 (0.00)
Mar	18-20	33	18 (0.55)	9 (0.27)	0 (0.00)	0 (0.00)	0 (0.00)	4 (0.12)	0 (0.00)
Apr	24-25	23	20 (0.87)	14 (0.61)	0 (0.00)	0 (0.00)	0 (0.00)	3 (0.13)	7 (0.30)
May	30-June 2	32	10 (0.31)	19 (0.59)	11 (0.34)	4 (0.13)	5 (0.16)	3 (0.09)	5 (0.16)
June	26-30	39	14 (0.36)	29 (0.74)	23 (0.59)	2 (0.05)	9 (0.23)	3 (0.08)	4 (0.10)

NR, Not Recorded.

ed. No pupae were observed from November 1995 to April 1996. In this period, we saw no adults during the census. The incidence of the 1st and 2nd instar larvae increased from March 1996. The incidence of the 3rd and 4th instar larvae increased in April and the first pupa of the season appeared in May.

The incidence of *A. albopictus* was also highest in August and decreased in September. In spite of the high incidence in August 1995, larvae of *A. albopictus* appeared in only a small number of the stumps in May 1996. The incidence of *A. japonicus* showed a peak in July 1995 and decreased in August. In the next spring, larvae appeared in March, nearly at the same time as the new hatching cohort of *T. bambusa*. However, its incidence was low. In May, *T. bambusa* was predominant over *A. albopictus* and *A. japonicus* in the number of larvae (2nd-4th instar) per stump (Fig. 1).

Besides 3 larvae in 2 stumps, which had survived the drought probably in the wet sediment, no 3rd or 4th instar larvae were found in February or March 1996 in stumps of Group B+C (Fig. 2). The number of larvae in stumps of Group A gradually decreased from November 1995 to March 1996. Probably, two stumps of

Fig. 1. Frequency distributions of density (per stump) of the 2nd to 4th instar larvae of the three mosquito species in May 1996.

Fig. 2. Monthly changes in the total number of the 3rd and 4th instar larvae of *T. bambusa* in the study area during winter 1995–1996. Figures in parentheses indicate the number of water-filled stumps.

Group A, in which no *T. bambusa* larvae were found and only a little water existed in February, had dried up before February. In total, from November to March, the number of the overwintering 3rd and 4th instar larvae of *T. bambusa* in the study area decreased from 1208 to 225.

The larvae hatching from overwintering eggs were found in 23 of the 33 stumps which held water in March or April 1996 (Fig. 3). At least 12 of them had dried up in winter (Group B–D), indicating that the diapause eggs of *T. bambusa* have resistance to desiccation. However, the larvae from the overwintering eggs existed more frequently in the stumps which had held water persistently (Fig. 3; $df=3, \chi^2=11.73, P<0.01$). The overwintering eggs were concentrated in stumps which held water in September and October 1995 (Table 3).

Figure 4 shows the number of *T. bambusa* immatures (2nd instar-pupae) in the early breeding season 1996. The total

Fig. 3. Number of the bamboo stumps with (above) and without (below) *T. bambusa* larvae from overwintering eggs in March–April 1996.

Table 3. The relationship between the distribution of overwintering eggs of *T. bambusa* and the status of stumps in September and October 1995.

Status of the stump in Sept and Oct	n*	Larvae from overwintering eggs	
		Observed	Not observed
With water	19	19	0
Without water	12	3	9

Fisher's exact test, $P<0.001$

* 2 stumps labeled in November 1995 were excluded.

number of immatures, except 1st instars, was largest in May, being 2994. The combined number of immatures in the stumps that had dried at least once in winter (Group B–D; 1544) contributed to about a half of the total number of immatures in the study area in May. The number of immatures in the stump of Group A ($n=12$, $\text{mean} \pm \text{SD} = 120.8 \pm 121.4$) and Group B ($n=8$, 179.6 ± 309.5) did not differ significantly in May (Mann–Whitney *U*-test, $P>0.5$). However, the number in Group C+D ($n=12$, 8.9 ± 25.3 per stump) was sig-

Fig. 4. Total number and stage structure of *T. bambusa* immatures in stumps of three categories from April to June 1996. Figures in parentheses indicate the number of water-filled stumps.

nificantly lower than that in Group A and B ($P < 0.01$ for both) in May.

The number of *T. bambusa* immatures (2nd instar-pupa) in May 1996 was not correlated significantly with the number of leaves trapped in the stump from April to May (Fig. 5; Spearman's rank correlation, Group A+B: $n = 20$, $r_s = -0.182$, $P > 0.4$; Group C+D: $n = 12$, $r_s = -0.051$, $P > 0.8$). However, the combined number of pupae in May and June 1996 in the stumps of Group A+B was positively correlated with the number of leaves that had been trapped from April to June (Fig. 6; $n = 20$, $r_s = 0.475$, $P < 0.05$). On the contrary, the number of larvae (2nd–4th instar) in June in Group A+B stumps was negatively correlated with the number of leaves (Fig. 6; $n = 18$, $r_s = -0.564$, $P < 0.05$). In the stumps of Group C+D, no significant correlation was detected either between the

Fig. 5. Relationship between the number of leaves trapped in the stump from April to May 1996 and the total number of *T. bambusa* immatures (2nd instar-pupa) in May.

total number of pupae and that of leaves (Fig. 6; $n = 21$, $r_s = -0.041$, $P > 0.8$) or between the number of larvae in June and that of leaves ($n = 21$, $r_s = -0.022$, $P > 0.9$).

DISCUSSION

The present study showed that the overwintering success of *T. bambusa*, either as larva or egg, was influenced by drought. Since the larvae were susceptible to desiccation, success or failure of overwintering of *T. bambusa* larvae was primarily determined by whether the stump had dried up in winter. From November 1995 to March 1996, overwintering larvae disappeared in more than a half of the stumps due to drought and the total number of the 3rd and 4th larvae decreased to less than a quarter.

However, the reduction in the number of larvae during winter, was offset by the larvae that hatched from overwintering eggs. Presence of the larvae from the overwintering eggs in a large portion of water-filled stumps in spring, including those which had dried up in winter, indicated that the overwintering eggs of *T. bambusa* had some degree of desiccation resistance. However, the larvae from overwintering eggs existed more frequently in stumps

Fig. 6. Above, Relationship between the number of leaves trapped in the stump from April to June 1996 and the combined number of *T. bambusa* pupae found in May and June; Below, Relationship between the number of leaves trapped in the stump from April to June 1996 and the number of *T. bambusa* larvae (2nd-4th instar) in June.

which had held water persistently. It is yet to be studied whether the observed pattern in the distribution of overwintering eggs was due to the high mortality in drought-prone stumps or the oviposition site selection of adult females. Concentration of overwintering eggs in stumps which had held water in September and October suggests selection of water-filled stumps by gravid females as oviposition sites.

The number of *T. bambusa* larvae (2nd-4th instar) increased after the new hatching cohort appeared in March 1996, and

reached 2994 in May. We did not count the exact number of 1st and 2nd instar larvae that had overwintered. However, since the density of them was low and the total number was less likely to exceed that of the 3rd instar larvae in February (80, in total), it is probable that the total number of overwintering larvae that survived to February was less than 305 (225+80). Thus, the contribution of the overwintering larvae to the total number of individuals in the beginning of the new breeding season can be estimated as about 10%. Makiya (1968) reported that, in southern Kyushu, overwintering eggs of *T. bambusa* contributed more to the spring population than the overwintering larvae. The present study confirms his findings and further suggests that the importance of overwintering eggs would become greater as winter drought becomes greater, because of their resistance to desiccation. In our results, about a half of the immatures in May were in stumps that had dried at least once in winter.

The positive correlation between the number of leaves and the total number of pupae in stumps of Group A + B suggested that pupation of *T. bambusa* was partially limited by the availability of food resources (decaying leaf litter and associated microorganisms) in persistent bamboo stump pools. The negative correlation between the number of leaves and the number of resident larvae in June also suggested the developmental delay and resultant high larval density in stumps with few leaves.

In the bamboo grove, *T. bambusa* coexists with several mosquitoes. Of them, *A. albopictus* is the most abundant. Mori and Wada (1978) observed that *A. albopictus* larvae from overwintering eggs appeared by mid-April and the larval density increased drastically after mid-May in artificial containers in Nagasaki, western Kyushu. In the present study, *A. albopictus* larvae appeared in only a small number of stumps in May or June 1996, in spite of the high incidence in August 1995.

The overwintering of *A. albopictus* in the present study appeared to be relatively unsuccessful. As eggs of this mosquito can overwinter even in northern Japan (Hanson, 1995) and have high desiccation resistance especially when they enter diapause (Sota and Mogi, 1992), it is less likely that coldness or drought causes the high mortality of overwintering eggs of *A. albopictus*. The low incidence of *A. albopictus* in the spring might be explained with the drought in the previous autumn. Mori *et al.* (1981) reported that diapausing eggs increased from mid-September in Nagasaki. In the present study, drought in mid-September 1995 reduced the number of water-filled stumps, and the incidence of *A. albopictus* declined drastically after this period. It is possible that *A. albopictus* population could not produce a sufficient number of overwintering eggs before the population size was reduced. *Aedes japonicus*, which was not dominant in the bamboo grove in 1995, appeared nearly at the same time as *T. bambusa*, but the incidence and the density was low.

How are the overwintering processes important in determining the relative dominance of mosquitoes in a bamboo grove? The low incidence of *A. albopictus* and *A. japonicus* in early spring, both of which are potential competitors of *T. bambusa*, might be favorable for the population growth of *T. bambusa*. Sunahara and Mogi (1997) experimentally showed that (1) *A. albopictus* was superior to *T. bambusa* in the short-term competition, as the former could grow and exploit food resources more rapidly than the latter, and (2) *T. bambusa* larvae could survive and grow better than *A. albopictus* in the later stage of long-term competition when food resources were strongly limited. The present study showed that *T. bambusa* larvae which had overwintered as either larva or egg were present when *A. albopictus* larvae appeared in spring. They could grow without the major competitors in this critical period for the population growth in the new breeding season. The

prior occupation of bamboo stumps by *T. bambusa* in the early breeding season may negatively affect the subsequent population growth of *A. albopictus* and other mosquitoes, especially in stumps with little leaf input, and facilitate the predominance of *T. bambusa* in the bamboo grove.

Successful overwintering can be attained when (1) a sufficient number of diapausing individuals is produced, (2) overwintering population survives well, and (3) the population growth can restart in a favorable condition earlier in the new breeding season. The overwintering of *T. bambusa* reported in the present study appeared to be fairly successful, by satisfying these conditions with (1) predominance of larvae in bamboo stumps in the late autumn, (2) desiccation resistance in overwintering eggs, and (3) appearance of larvae from overwintering eggs in the early spring, before other mosquitoes become abundant.

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摘 要

竹林におけるキンパラナガハシカ (Diptera: Culicidae) の幼虫および卵の越冬成功におよぼす乾燥の影響

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佐賀市近郊の竹林において、冬季の乾燥がキンパラナガハシカの幼虫および卵の越冬におよぼす影響を調べた。1995年11月に3,4齢幼虫の見られた竹の切り株のうち半数は冬季に乾燥し、幼虫のほぼ全数が死亡した。調査区域内の3,4齢幼虫の全数は11月から翌年の3月にかけて1208個体から225個体に減少した。越冬卵から孵化した幼虫が出現した3月以降、幼虫の出現頻度は増加し、5月には調査区域内の2齢幼虫から蛹までの総個体数は2994に達した。これらのうち約半数は、冬季に乾燥したことのある切り株内に存在しており、キンパラナガハシカの越冬卵が乾燥耐性をもつことが示された。キンパラナガハシカの幼虫は春期に、ヒトスジシマカやヤマトヤブカが増加する以前に高密度になり、主な競争者が不在のうちに成長することが可能であった。キンパラナガハシカのこのような越冬様式は、竹林内で本種の優占を促進するものと考えられる。