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Larval Performance and Niche Separation between Two Synhospitalic Species of *Colocasiomyia* (Diptera, Drosophilidae)*

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Abstract *Colocasiomyia alocasiae* and *C. xenalocasiae* are synhospitalic, floricolous species that separate their larval niches micro-allopatrically in the same host inflorescence of *Alocasia odora*. Both species showed density-dependent scramble type of competition for larval food. Survival rate of larval period and puparium size both decreased sharply at high densities in both species. Niche separation in host inflorescence may prevent larvae of the two species from scrambling.

Key words Larval performance, Synhospitalic drosophilids, Scramble type of competition, Araceae

Introduction

Correlations between ovipositing preference and offspring performance are an important factor for insects that use particular plant species as hosts (Fox 1993; Schorrocks *et al.* 1990; Singer *et al.* 1988; Via 1986). The floricolous drosophilids, *Colocasiomyia alocasiae* (Okada 1975) and *C. xenalocasiae* (Okada 1980), Drosophilidae, are a "synhospitalic" pair (see Okada 1980) that exists in the same host inflorescence of *Alocasia odora* C. Koch, Araceae. This host is distributed in Okinawa and Taiwan.

Females of the two species oviposit many eggs in the same inflorescence simultaneously. Strong intra- and/or interspecific local competition between larvae may be expected.

In this paper, I examine the interspecific effects of density within the synhospitalic pair on larval performance of both species.

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Materials and Methods

Larval performance was measured by survival rate, pupal size and development time. Eggs examined were collected from fresh inflorescences in which wild females were allowed to oviposit for a few days in the laboratory.

Experiment 1. Low density : one species (control) --- Thirty eggs of each species were placed in a petri dish (6 × 1.5 cm) with 0.3-0.35 g of fresh tissue of host inflorescence on 15% agar bait. A fresh piece of male tissue was used for *C. alocasiae*, while a sterile piece of tissue was used for *C. xenalocasiae* (Fig. 1). There were 10 replicates for *C. alocasiae* and 9 for *C. xenalocasiae.*

Experiment 2. Low density : two species --- To examine the effect of presence of the other species in the synhospitalic pair, 10 eggs of each of the species were placed in a petri dish together with 0.3-0.35 g of sterile host tissue. This is because larvae of both spieces coexist naturally in the sterile part of the host inflorescence. Six replicates were made.

Experiment 3. High density : one species --- Two hundred eggs of each species were placed in a petri dish with the same amount of larval food as in Exp. 1 and 2. There were five replicates for each species.

Experiment 4. High density : two species --- One hundred eggs each of the species were placed together. Then a total of 200 eggs were put in a petri dish under the same condition as in Exp. 3. Eight replicates were made.

Eggs were allowed to hatch and to develop under laboratory conditions (24-26˚C). The number of unhatched eggs were counted every day to estimate the survival rate of the egg stage. Larvae of both species pupate in agar medium, so puparia were counted every day. Puparium size (Fig. 2) was measured under a binocular microscope after emergence. The emerging adults were counted every evening. All experiments were done from April to June, 1992.

Results

Effects of density on larval performance

Larval performance was compared by survival rate in the preimaginal period, puparium size, and development time from egg to adult in low and high densities. The results are summarized in Table 1, and statistical analysis on survival rates and puparium sizes by Scheff's test are in Table 2.

Survival rate

In Exp. 1 (control), the survival rate of egg stage, i.e., hatchability, was very high in both species. In *C. alocasiae*, two of ten replicates showed 100% of hatchability. Three of nine replicates in *C. xenalocasiae* also showed 100% success. The survival rate of the larval stage, given by pupation rate, was also high in both species. The range of pupation

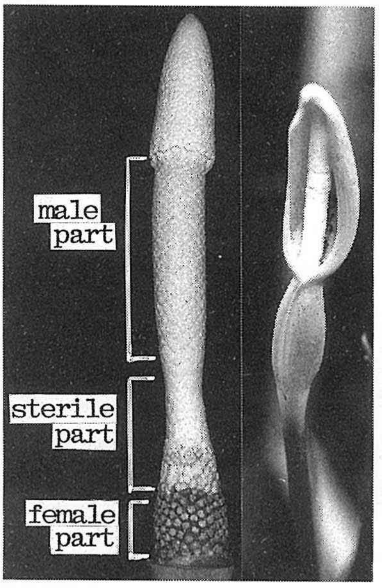

Fig. 1. Right, inflorescence of the host plant species, *Alocasia odora* C. Koch, Araceae, in bloom (photo by Kazuo Minato). Left, spadix without spathe showing the three parts of inflorescence.

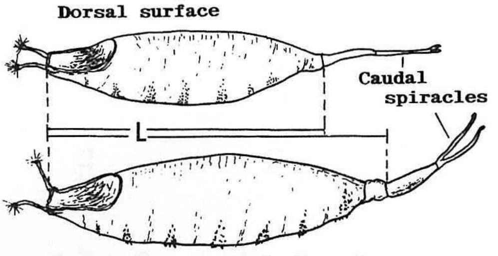

Fig. 2. Puparium size (L) was measured as length from apex to the posterior end of the body without caudal spiracles. *Colocasiomyia alocasiae* (upper) and *C. xenalocasiae* (lower).

rate was 70% to 100% in *C. alocasiae* and 65.4% to 100% in *C. xenalocasiae*. Almost all pupae emerged successfully in both species. Only one pupa of *C. alocasiae* and six pupae of *C. xenalocasiae* failed to emerge. The survival rate throughout the preimaginal period was also very high at low densities for both species. Although it was higher in *C. alocasiae* than in *C. xenalocasiae*, the difference was not significant (Mann-Whitne's Ucal=27, p>.05).

Exp. 2. When bred together in the same petri dish at low density, the preimaginal survival rates of both species were equally high, and also equalled the rate shown in Exp. 1. All eggs successfully hatched and all pupae could emerge. Mortality occurred only in the larval stage in both species, but viability was not influenced by the presence of larvae of the other species that was using the same food resource. There were no significant differences of survival rates between the species, or between the control (Exp. 1) and this experiment (Table 2).

Table 1. Offspring survivorship and puparium sizes of *Colocasiomyia alocasiae* and *C. xenalocasiae* at low and high densities.

	C. alocasiae					*C. xenalocasiae*				
Conditions	N[1]	n[2]	Survival rate by petri dish ave. ±SE (%)	n	Puparium size ave. ±SE (mm)	N	n	Survival rate by petri dish ave. ±SE (%)	n	Puparium size ave. ±SE (mm)
Ex. 1. Low density : one species (control)										
Egg (hatchability)	10	300	95.3± 3.9			9	270	93.3± 7.1		
Larva (pupation rate)	10	286	90.0±10.3			9	252	84.3±10.8		
Pupa (emergence rate)	10	261	99.6± 1.2	258	2.60±0.01	9	212	97.3± 6.9	206	3.33±0.28
Total (egg-adult)	10	260	86.7±10.7			9	206	76.3±10.7		
Ex. 2. Low density : two species										
Egg	6	60	100			6	60	100		
Larva	6	60	83.3±10.3			6	60	83.3±19.7		
Pupa	6	50	100	50	2.54±0.05	6	50	100	50	3.34±0.07
Total	6	50	83.3±10.3			6	50	83.3±19.7		
Ex. 3. High density : one species										
Egg	5	1000	98.4± 2.0			5	1000	81.8±13.6		
Larva	5	984	18.2± 6.1			5	818	34.1±14.5		
Pupa	5	177	98.2± 3.0	177	2.04±0.23	5	269	60.0±28.7	262	2.39±0.14
Total	5	178	17.7± 6.2			5	176	17.6±12.0		
Ex. 4. High density : two species										
Egg	8	800	96.8± 2.0			8	800	88.8± 8.1		
Larva	8	774	42.9±28.1			8	710	24.2±14.9		
Pupa	8	332	95.4± 5.6	282	1.92±0.12	8	172	95.5± 5.2	167	2.13±0.12
Total	8	318	39.8±26.3			8	164	20.5±13.3		

1) number of replicates; 2) number of individuals examined

Table 2. Results of multiple comparison in survival rate of pre-imaginal period and puparium size of *Colocasiomyia alocasiae* and *C. xenalocasiae*. Probabilities were obtained by Scheff's test.

		C. alocasiae				*C. xenalocasiae*			
	Exp.	1	2	3	4	1	2	3	4
Survival rate of pre-imaginal period	1	-	99.42	0.51	3.27	-	98.16	4.17	0.80
	2		-	2.98	14.30		-	3.36	0.85
	3			-	81.44			-	99.97
	4				-				-
Puparium size	1	-	58.19	1.20	0.02	-	98.55	12.07	0.05
	2		-	35.54	9.67		-	31.27	0.81
	3			-	97.42			-	66.92
	4				-				-

Exp. 1, low density : one species (control); Exp. 2, low density : two species; Exp. 3, high density : one species; Exp. 4, high density : two species.

Exp. 3. A drastic reduction in survival rate occurred at high densities. In *C. alocasiae*, this occurred in the larval stage. Only 177 of 984 larvae could pupate under high density. The lowest pupation rate among five replicates was 10.5%. In *C. xenalocasiae*, a similar reduction of survival rate was detected: only 269 of 818 larvae pupated. The emergence rate was lower; about 40% of pupae died before emergence.

The results were clear: 1) preimaginal survival rate significantly decreased in both species when larvae were bred under competitive conditions for food; and 2) the presence of the other species did not influence survival rate.

Puparium size

The average puparium size of *C. alocasiae* was smaller than that of *C. xenalocasiae* in all experiments, because *C. alocasiae* is a smaller species in nature (Yafuso 1993). In *C. alocasiae*, the average size was 2.5-2.6 mm at low density (Exp. 1 & 2). The size decreased 0.5 mm or more when bred in high density (Exp. 3 & 4). The reduction was highly significant between Exp. 1 and Exp. 3, and also between Exp. 1 and Exp. 4. Surprisingly, the differences were not significant between Exp. 2 and Exp. 3 or 4 by Scheffe's test. I note, however, that the differences between Exp. 2 and Exp. 3 and also between Exp. 2 and Exp. 4 were highly significant by Mann-Whitney's test (Ucal=0, $p<.01$ in both cases).

C. xenalocasiae, the puparium size was about 3.3 mm in low density and decreased 1 mm or more at high density. In spite of this large difference, it was not significant by Scheffe's test, but was highly significant by Mann-Whitney's test (Ucal=0, $p<.01$).

Thus, a large reduction in puparium size was detected under competitive breeding condition for larval food in both species.

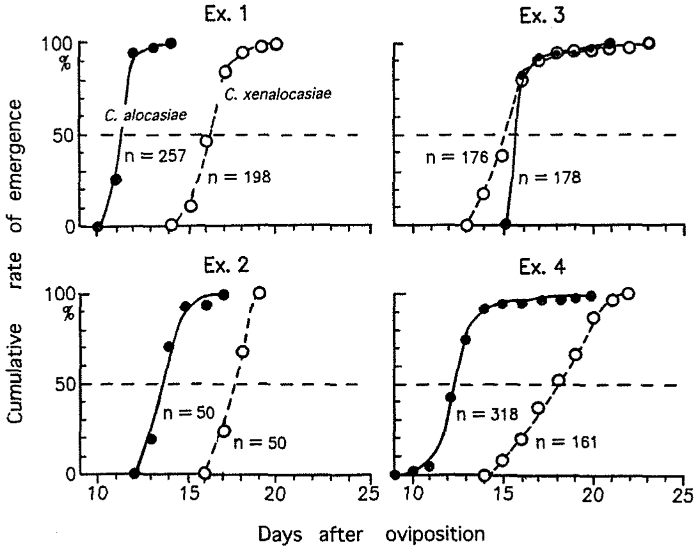

Fig. 3. Effects of density on development time indicated by the 50% cumulative rate of emergence. Solid circle, *C. alocasiae*; open circle, *C. xenalocasiae*.

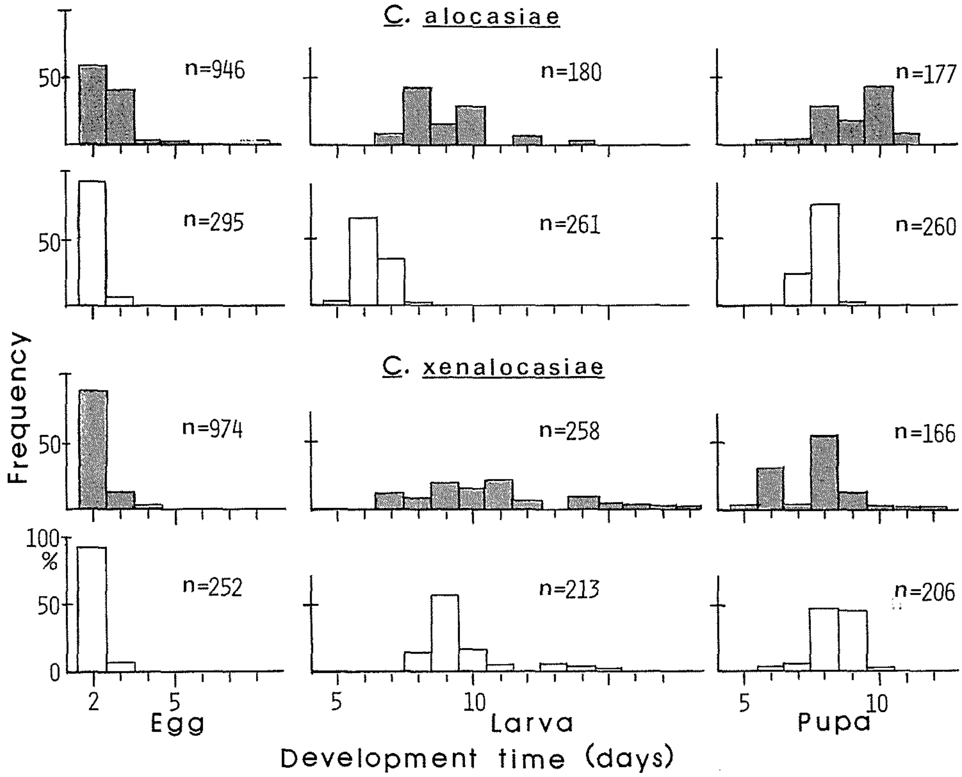

Fig. 4. Development time of each stage of preimaginal period. Solid column, high density; open column, low density.

Development time

Development time after oviposition assessed by a 50% cumulative rate of emergence is illustrated in Fig. 3. Development times of *C. alocasiae* were 11.5 (Exp. 1) and 13.5 days (Exp. 2) at low density. When bred at high density, it was delayed four days in Exp. 3, but changed little in Exp. 4 (12.3 days). In *C. xenalocasiae*, it was 16 (Exp. 1) and 17.5 days (Exp. 2), and 15.5 (Exp. 3) and 18 days (Exp. 4), respectively.

In contrast, development time of each development stage showed a remarkable influence of density (Fig. 4). Egg period in the two species was only two days at low density. A few eggs hatched three or four days after oviposition at high density. Larval period of *C. alocasiae* was five to eight days with a distinct peak on the sixth and seventh days at low density. It was prolonged until 7 to 14 days, with a peak delayed 3 or 4 days. In *C. xenalocasiae*, larval period was 8 to 15 days with a sharp peak on the ninth day at low density. In spite of early initiation of pupation, the larval period was prolonged until 18 days at high density. A distinct peak disappeared and even emergence continued for nearly two weeks. A small number of larvae pupated day by day. The following pupal stage was also prolonged at high density in both species.

Discussion

Larval stages have several competitive factors among monophagous flower-breeding drosophlids (Kambysellis & Heed 1971; Montague 1984; Montague & Kaneshiro 1982). Pipkin *et al.* (1966) reported that closely related monophagous *Drosophila* species depend on the same host plant in different geographical areas, while two monophagous flower-feeders use two different host plant species in the same area. Budnik & Burncic (1983) described how two drosophilid species that shared many ecological and behavioural characteristics expanded their population at different times of year, thus preventing strong interspecific competition.

Lacking such a geographic or seasonal separation, *C. alocasiae* and *C. xenalocasiae* coexist in the same host infloresence at the same time. Significant reductions were detected in the survival rate of larvae and puparium size between the control and the treatments of high density in the two species. Both species produced fewer and smaller offspring when bred under competitive conditions. These reductions in viability and size indicate that the two species exhibited the scramble type of competition for larval food (Ito *et al.* 1992).

I did not examine the influence of metabolic wastes on larval performance of the two synhospitalic *Colocasiomyia* species, but it is possible that high density condition may exert a negative effect on survival and growth.

Niche separation in a host inflorescence may act to prevent the two specialist floricolous species from catastrophic reduction of the population in the limited larval food resource and enable them to coexist in synhospitalism in the same host inflorescence. Density dependent control of oviposition by females of the two species should be investigated in future studies.

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