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Relationship Between Flowering of Wild Rice and Larval Mosquito (Diptera: Culicidae) Abundance in California

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ABSTRACT Densities of larval *Culex tarsalis* Coquillett and *Anopheles* spp. populations were monitored in experimental plots of white rice, *Oryza sativa* L., and wild rice, *Zizania palustris* L., in Lake County, CA, during the spring and summer of 1989. Plant height, floral debris drop, water quality, and bacterial counts were measured and contrasted between the two systems. *Anopheles* spp. and *C. tarsalis* populations in wild rice were 6 and 2.6 times higher, respectively, than in the white rice over the entire season. A significantly greater number of notonectids and hydrophilid larvae were sampled in the wild rice treatments and did not appear to be responsible for the difference in larval mosquito populations. A positive correlation was found between average larval density and plant height for *Anopheles* spp. in both wild and white rice and for *C. tarsalis* in wild rice during the early growing season. In the latter half of the growing season, only *Anopheles* spp. densities showed a significant correlation with plant height. A significant positive correlation was demonstrated between the number of shed wild rice anthers and larval densities for both *Anopheles* spp. and *C. tarsalis*. No significant differences were noted in either water quality factors or bacterial counts between white and wild rice treatments. In the field, development of *C. tarsalis* larvae was slower in wild rice than in white rice plots before flowering but faster during flowering. However, temperature-adjusted developmental times were significantly shorter for the wild rice group only during flowering. In the laboratory, *C. tarsalis* completed development from second instar to adult when fed only wild rice pollen. These results suggest that wild rice pollen serves as a nutrient source for larvae in the field. In addition, the floral components of wild rice may serve as an oviposition attractant and structural refuge for the immature stages.

KEY WORDS mosquitoes, populations, wild rice

WILD RICE, *Zizania palustris* L., is grown commercially in California's Central Valley and to a lesser extent in Lake, Mendocino, Shasta and Lassen counties. White rice, *Oryza sativa* L., is grown only in the Central Valley, and both wild and white rice are often planted in adjacent fields. Both rice mesocosms have been shown to be important larval habitats for several species of mosquitoes, including *Anopheles freeborni* Aitken and *Culex tarsalis* Coquillett (Kramer & Garcia 1987, 1988). In the Central Valley, larval mosquito populations were 4–8 times higher in wild rice than in white rice, and *C. tarsalis* larvae developed faster in wild rice. These investigators suggested that the higher numbers of mosquitoes observed in wild rice in late July and August was caused in part by a higher nutrient load in the water. Although they suggested that plant debris shed by wild rice was responsible for this enrichment, they did not quantify this relationship. They also suggested that faster development could lead to a greater number of generations in wild rice, thus fostering higher mosquito populations (Kramer & Garcia 1987, 1988).

In 1989, Kramer & Garcia analyzed the relationship between mosquito abundance and a variety of biological, chemical, and physical factors measured in 20 commercial wild rice fields in Lake County. Plant height and floating algal density accounted for 78% of the variance in mosquito abundance in the early season, whereas fish abundance, plant density, and algal density accounted for 44% of the mosquito population variance later in the season.

Unlike white rice, wild rice plants grow rapidly to >2 m, and produce a large floral head which sheds pollen and male spikelets for ≈10 d. Because of continued production of new tillers, a wild rice field sheds pollen and other floral parts for several weeks. These floral parts remain on the water surface, apparently adding nutrients, and perhaps providing oviposition attractants and refuge for mosquito larvae from predators, as demonstrated for emergent and floating vegetation (Orr & Resh 1989). The relationship be-

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ween mosquito density and the amount of debris shed by wild rice during flowering has not been determined.

This study compares the colonization rates and abundance of larval mosquitoes in wild and white rice mesocosms in relation to plant growth and floral debris drop. Also, preliminary experiments were conducted to test the potential role of wild rice pollen as a nutrient source for *C. tarsalis* larvae.

Materials and Methods

Study Plots. The study was conducted in experimental wild rice plots maintained by the Lake County Mosquito Abatement District (Kramer et al. 1987, 1988). Each plot was supplied with water from a common source through a separate inlet pipe covered with a fine-mesh bag to exclude fish eggs. The outlet control boxes were screened to prevent invasion by fish from the return ditches. Because of prevailing northwesterly winds, white rice was planted in the three upwind plots to minimize contamination by wind-blown plant materials from adjacent wild rice plots. Wild rice treatments were randomly assigned to 3 of the remaining 15 plots. The remainder of the plots were used in experiments unrelated to those reported here. All plots were flooded on 18 May 1989. White rice (variety M202) and wild rice seeds were sown by hand on 21 and 25 May at rates of 240 and 185 kg/ha, respectively. Water levels in the wild rice were kept at 20 cm. Water levels in white rice plots were gradually increased in relation to plant growth, as recommended for this variety. Water levels in all plots were similar after 4 wk.

Mosquito Sampling. Larval mosquitoes were sampled with standard 400-ml dippers weekly from 25 May through 28 September. White rice could not be sampled until the third week because of the initially shallow depths. Three-dip samples were taken at seven randomly selected stations along three transects on the edges of each pond (21 dips per transect, three transects per pond). Larvae from each transect were identified to genus and counted in the field. Larvae were classified as early (first and second) or late (third and fourth) instars. Portions of each sample from 9 August through 28 September were preserved in 70% ethanol for identification to species in the laboratory. The ratios of *A. freeborni* and *A. franciscanus* McCracken in wild and white rice fields were analyzed with the chi-square test.

Predator Sampling. Larger predators were sampled with minnow traps (3.2 mm mesh), and smaller organisms with bottle traps constructed from 0.95-liter (1 qt) jars fitted at the mouth with a plastic funnel. A hardware cloth (3.2 mm mesh) barrier over the mouth of the bottle traps excluded larger predators. Traps were placed on the bottom, parallel to and 1–2 m from shore. Traps were placed on each side of each field, and the contents were counted after 24 h. Organisms were identified to family level, and seasonal averages were compared using Student's *t* test for each predator group.

Plant Growth and Debris Sampling. Plant height was measured by comparison with 3-m PVC pipes marked at 10-cm intervals and placed in five permanent, randomly selected stations in each plot. Following the first observed flowering in wild rice, five debris samplers were floated on the water surface of each white and wild rice plot. Each sampler consisted of a plastic 2,000-ml container (210 cm^2 area) lined with a plastic bag. Debris samplers were placed at five randomly selected stations and replaced weekly. After the anthers were counted, the entire sample was dried and weighed. The last debris samples from wild rice were taken on 14 September, after which rainfall and extensive lodging prevented further monitoring. White rice debris samples were obtained until 28 September.

Regression Analysis. The average density (larvae per dip) for both *Anopheles* spp. and *C. tarsalis* was paired with the average plant height or anther count (anthers per trap) for each treatment. The analysis of larval density versus plant height included all values from 21 June until 95% of maximum plant height was reached (16 August). A simple linear regression of these data was conducted using the regression operation of Lotus 123 version 2.01 (Lotus Development, Cambridge, MA). Mosquito populations in white and wild rice were compared using Student's *t* test.

Water Quality Analyses. A 200-ml water sample was taken from each plot near the outlet box every other week. Conductivity, pH, turbidity, alkalinity, nitrate, phosphate, and chemical oxygen demand were measured using standard methods (Greenberg 1985). Total heterotrophic bacteria were estimated using Biosperse test strips (Ecologic Instrument Division, I.M.E., Bohemia, L.I., NY). Water quality parameters from wild and white rice for individual dates were compared with Student's *t* tests.

Larval Development (Field). Larvae were hatched in the laboratory from egg rafts obtained from field-collected *C. tarsalis* and reared to the second instar on Tetramin (TetraWerke, Melle, Germany) fish food. Five second instars from even-aged cohorts were placed in uncovered developmental cages (Kramer & Garcia 1988). Five cages were floated in each wild and white rice plot. Each cage was observed daily, and the number and instar of surviving larvae were recorded. Cohorts were set before (14–28 July) and during (28 July through 14 Aug) observed flowering of wild rice. A temperature probe from a weather logger (OWL, EME Systems, Berkeley, CA), which recorded hourly, was placed just be-

low the surface in one developmental cage in each pond. The total degree-days above the threshold of 9.1°C (Miura & Takahashi 1988) were calculated for each development period. The minimum threshold reported in this paper was 9.0°C, but our analysis of their data calculates a threshold of 9.1°C, which was used in our calculations. Development was compared between the two rice treatments using Student's *t* test. Analyses compared development in both number of days and number of degree-days.

Larval Development (Laboratory). Development of *C. tarsalis* larvae fed with wild rice pollen or a standardized diet was compared in the laboratory. A pollen suspension was obtained by washing mature flower heads from field-collected wild rice and straining it through fine fabric (200-μm aperture). The pollen density (10^5 grains per ml) was determined with a standard hemocytometer. The standard diet consisted of eight parts Tetramin flakes, four parts rat chow, four parts brewer's yeast, and one part liver powder (Dadd et al. 1988). Six replicates of 100 second instars each were placed separately into six enamel pans (45 by 25 cm) each containing 1.5 liter tap water. A slurry of laboratory diet (0.5 g in 10 ml of water) was added to three control replicates every 3 d, and 10 ml of the refrigerated pollen suspension was added to the other three containers daily. Both treatment groups were kept in the same room at 22°C and a photoperiod of 16:8 h (L:D) for the duration of the experiment.

The first 30 pupae from each replicate were removed, weighed, and held in individual vials for measurement of wing lengths of the first 10 associated adults of each sex. Pupae were lightly blotted on filter paper to remove excess water and weighed to ±0.1 mg. The left wings were removed from the resulting adults, mounted on a microscope slide moistened with soapy water, and measured with a dissecting microscope equipped with an optical micrometer. The straight line distance from the alular notch to the end of the wing (excluding fringe hairs) was measured to ±0.1 mm, as described by Bock & Milby (1981).

Results

Plant Growth and Debris Sampling. Wild rice reached maximum average height in mid-August at 175 cm (Fig. 1). Growth from late June to mid-August averaged 15 cm/wk. White rice grew slower (8 cm/wk) and reached its maximum average height (90 cm) in mid-August. Flowering was first observed in wild rice on 19 July, and shed anthers were first detected on 26 July. Anther density peaked in mid- to late August, then rapidly decreased (Fig. 1). Wild rice anthers were shed ≈1 wk after dropping their pollen. Other parts of the spikelet (glumes, seeds, etc.) fell later in the season. By late season, few anthers were collected, although other parts of the male spikelets and seeds became more numerous in the debris samples. In white rice, flowering was not observed until mid-August, and white rice anthers were observed in only the final three samples of the study (7–28 September).

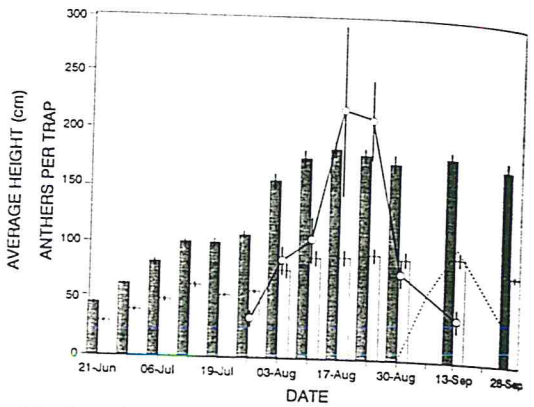


Fig. 1. Plant height (bars; mean ± SEM) and anther drop counts (lines) from wild and white rice ponds, Lake County, CA, 1989. Wild rice is denoted by the filled bars and solid line.

Mosquito Populations. *Culex tarsalis, A. franciscanus,* and *A. freeborni* larvae were first detected in white rice plots on 21 June and in all plots by 28 June (Fig. 2). *A. freeborni* was the most abundant mosquito in the wild rice plots.

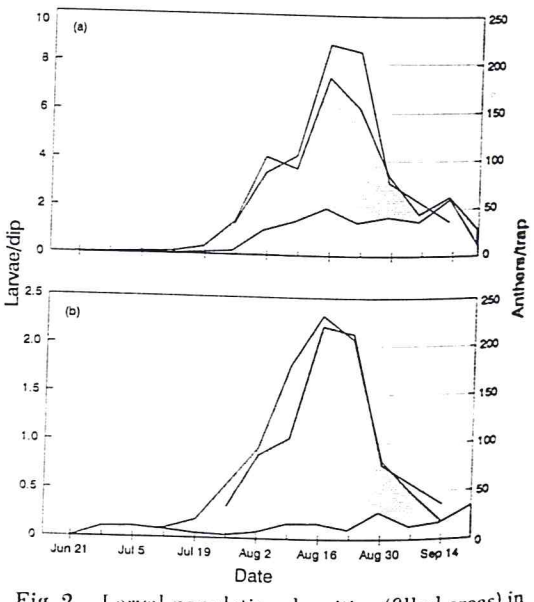
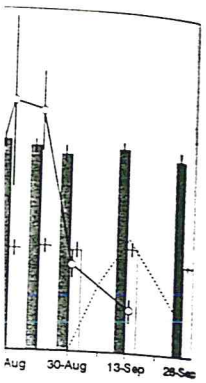


Fig. 2. Larval population densities (filled areas) in wild and white rice compared with anther drop (thick line) from wild rice ponds. Wild rice populations are denoted by filled pattern. (a) Anopheles spp. (b) *C. tarsalis.*



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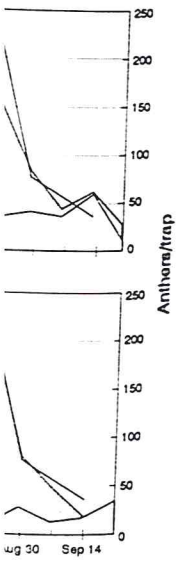

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whereas *C. tarsalis* and *A. franciscanus* were common but at lower densities. Regardless of species, numbers of early and late instars were significantly higher in wild rice than in white rice (Table 1). In wild rice, *C. tarsalis* and *Anopheles* spp. both peaked in mid-August at 2.25 and 7.25 larvae per dip, respectively. Population peaks of both genera in white rice were much lower (0.34 and 2.52 per dip, respectively), and remained relatively constant throughout the season (Fig.2). August ratios of *A. freeborni*/ *A. franciscanus* larvae were ≈2:1 in wild rice and 9:1 in white rice.

Larval abundance showed a positive linear relationship with plant height for *Anopheles* spp. in wild and white rice (r = 0.8973 and 0.8807, respectively; df = 7; P< 0.001), and for *C. tarsalis* (r = 0.8972 and 0.6580, respectively) from floating stage to maximum height.

Predator Populations. Significantly higher populations of hydrophilid larvae (primarily large *Tropisternus lateralis* (F.) and *Hydrophilus triangularis* (Say) in the minnow traps, and notonectids (primarily *Buenoa* spp. and *Notonecta* spp.) in the bottle traps were found in the wild rice fields (t = 2.03 and 2.66, respectively; $P < 0.05$). There were no significant differences in other predator populations between wild and white rice fields (Table 2).

Relationship Between Larval Abundance and Floral Debris. There was a significant positive correlation (df = 6, $P < 0.05$) between the average number of wild rice anthers per sample and average number of both *Anopheles* spp. (r = 0.9708) and *C. tarsalis* (r = 0.9311) larvae per dip in wild rice over the entire season. No significant relationship between mosquito densities and white rice anthers was found (r = 0.5526 [*C. tarsalis*], 0.4424 [*Anopheles* spp.]; df = 7; $P >$ 0.05). There was no significant linear relationship between debris weight and density of *C. tarsalis* or *Anopheles* spp. (r = 0.4636 and 0.1732, respectively; df = 6; $P > 0.05$).

The ratio of early-/late-instar *Anopheles* spp. (4,362:2,473) was significantly lower in wild rice than in white rice (1,609:606) (1.76 versus 2.66; χ^2 = 74.67, df = 1, $P < 0.005$). No significant differences were found for any of the water quality parameters, including the bacterial counts, between white and wild rice ($P > 0.05$).

Table 1. Total numbers of early- and late-instar *C. tarsalis* and *Anopheles* spp. in wild and white rice over the entire season

Species	Stage	Wild rice	White rice	Wild/white rice ratio
C. tarsalis	Early instars	1,090	192	5.7:1
	Late instars	700	101	6.9:1
Early/late ratio		1.6:1	1.9:1	—
Anopheles spp.	Early instars	3,997	1,609	2.5:1
	Late instars	2,160	606	3.6:1
Early/late ratio		1.9:1	2.7:1	—

Larval Development in the Field. Fewer days were required for development of *C. tarsalis* from second instar to pupa in white rice during the preflowering period (Table 3; t = 3.84; df = 40; $P < 0.001$). During flowering, larval development was shorter in wild rice versus white rice (t = 2.32, df = 57, $P < 0.05$). Water temperatures were consistently cooler in the wild rice than in white rice. When development times were converted to degree-days >9.1°C, there were no significant differences (t = 1.44, df = 40, $P > 0.05$) between development times for larvae in white or wild rice during the preflowering period. No significant degree-day differences in larval development were found between flowering and preflowering (wild rice) periods in the white rice groups (t = 0.90, df = 31, $P > 0.05$). Development time in degree-days in the wild rice groups during flowering was significantly shorter than in the white rice group (t = 9.13, df = 57, $P < 0.001$) and the preflowering wild rice group (t = 5.92, df = 66, $P < 0.001$). Survivorship of larvae from the wild rice group was significantly higher ($P <$ 0.001) than from the white rice group during both periods of development (χ^2 = 43.94, df = 1) (Table 3).

Pupal weights from the pollen-fed group were about two-thirds those of the artificial diet group (Table 4). Wings were also shorter in the wild rice pollen group, and emergence success for

Table 2. Average number of potential predators per trap night (±SEM) in wild and white rice using two sampling systems

Organism	Fish traps			Bottle traps		
	Wild rice	White rice	t	Wild rice	White rice	t
Dytiscid adults	2.78 ± 0.43	3.45 ± 0.60	1.6473	0.82 ± 0.35	0.63 ± 0.35	0.8653
Dytiscid larvae	0.10 ± 0.05	0.22 ± 0.10	1.0281	1.42 ± 0.80	2.00 ± 0.77	1.2131
Hydrophilid larvae	1.53 ± 0.30	0.82 ± 0.19	2.0284*	0.72 ± 0.46	0.32 ± 0.23	1.7880
Notonectids	1.17 ± 0.30	1.81 ± 0.40	1.2894	0.33 ± 0.27	0.02 ± 0.04	2.6561*
Corixids	0.02 ± 0.02	0.12 ± 0.08	1.2937	—	—	—
Belastomatids	0.76 ± 0.13	1.12 ± 0.17	1.6734	—	—	—
Odonates	0.86 ± 0.22	0.53 ± 0.12	1.3019	0.32 ± 0.33	0.03 ± 0.05	1.9742
Flatworms	—	—	—	0.72 ± 1.06	0.93 ± 0.59	0.4135

Significant differences between wild and white rice treatments indicated by * ($P < 0.05$).

Table 3. Mean development times for two even-aged cohorts of 75 *C. tarsalis* from second instar to pupation

Cohort	Days ± SEM				Degree-days >9.1 °C ± SEM			
	Wild rice	*n*[a]	White rice	*n*[a]	Wild rice	Avg temp, °C	White rice	Avg temp, °C
Pre-flowering, 14–18 July	10.5 ± 1.5a	28	9.5 ± 0.5b	14	136 ± 18d	23.4	144 ± 8d	26.0
Flowering, 28 July–14 Aug.	10.7 ± 1.0a	40	11.8 ± 1.2c	19	115 ± 12e	21.0	148 ± 15d	23.1

Mean values followed by different letters are significantly different ($P < 0.001$).
[a] Number surviving to pupation.

both sexes combined was lower in the wild rice pollen group.

Discussion

Our studies verify the work Kramer et al. (1987, 1988) which noted higher numbers of *Anopheles* than *Culex* larvae in Lake County compared with Central Valley wild rice, and that mosquito larvae were much more abundant in wild rice versus white rice. This study also showed that the numbers of mosquito larvae in both wild and white rice in Lake County were several times the densities frequently recorded in these mesocosms in the Central Valley (Case-Lemenager et al. 1985; Case-Lemenager & Kauffmann 1986; Kramer & Garcia 1987, 1988).

Kramer & Garcia (1987, 1988) showed that larval mosquito densities in Central Valley wild rice rose abruptly in late July but remained relatively low and constant in adjacent white rice fields. Similar population curves were recorded in our study, indicating that these patterns were not peculiar to the Central Valley rice growing area and, in addition, could be demonstrated in small replicated plots. The higher mosquito populations in wild rice mesocosms did not appear to be the result of higher predation pressure in the wild white rice, because predator populations were either similar or higher in the wild rice plots.

Table 4. Average pupal weights, wing lengths, and emergence success of 300 *C. tarsalis* reared on diets of standard diet or wild rice pollen

Variable	Sex	Standard diet	Wild rice pollen
Pupal wt, mg	♂	3.41 ± 0.08	2.53 ± 0.13
	♀	4.58 ± 0.11	3.05 ± 0.02
Wing length, mm	♂	3.26 ± 0.03	3.02 ± 0.02
	♀	3.81 ± 0.08	3.28 ± 0.07
No. emerged	—	193	138
% Emergence	♂♂, ♀♀	64.3	46.0

Measurements are expressed as mean ± SEM of the first 10 individuals of each sex to emerge. Pupal weights and wing lengths within each sex were all significantly different between treatments (Student's *t* test, $P < 0.001$). Emergence is calculated from the number of adults developing from a total of 300 first instars.

Our study showed a shorter developmental period for *C. tarsalis* larvae in wild rice during flowering. Furthermore, higher survival rates of larvae in the floating cages were demonstrated in wild versus white rice. Kramer & Garcia (1987, 1988) also showed that caged *C. tarsalis* larvae developed more rapidly in wild than in white rice in the Central Valley. They suggested that the higher number of mosquitoes observed in wild rice in late July and August was caused in part by a greater nutrient load in the water. They suggested that the plant debris shed by wild rice was responsible for this enrichment. Our findings support the notion that greater nutrient enrichment is the most likely cause for the shorter development period and higher larval survival rate in the wild rice floating cages.

Regression analyses of debris weight versus larval mosquito density showed no significant correlation in either wild or white rice. The weight of the debris sample included not only anthers but also shed spikelets, seeds, and weed seeds. There was a significant positive correlation between the plant height and larval density in wild and white rice while the plants were growing.

Kramer & Garcia (1989) showed a strong correlation between larval abundance and early-season plant height, and later in the season with light penetration (i.e., plant density). In the early-season sampling period, a greater plant height would also have greater numbers of flowers undergoing anthesis, whereas the late-season correlation with plant density (a function of tillering) could be caused by formation of new flowers on those tillers. Thus, both the relationship to plant height and density could be explained as well by floral development.

When anther numbers in wild rice were compared with larval densities, a very high positive correlation was obtained. The significant correlation between plant height and mosquito density could have been coincidental, with anthesis occurring at about midgrowth. The lack of significant correlation between growth and larval density after maximum height was reached supports this suggestion.

The strong correlation between anthers and larval abundance in our study suggests a cause-

and-effect relationship, although it is clearly feasible that other nonquantified floral components may also be important. One such component that may be involved is pollen. Wild rice pollen would have been produced in direct proportion to anther development and maturity and would have been shed before the anthers dropped to the surface. If oviposition was in response to pollen density, the early-instar density would have been a result of oviposition occurring several days before anthers were sampled.

The higher ratio of late/early instars in the wild rice versus white rice suggests higher survival in the wild rice. Orr & Resh (1989) showed that emergent macrophytes not only provided refuge from predation for *Anopheles* larvae but also promoted higher survival in the absence of predation. The debris shed by wild rice flowers could play an important role in survival of mosquitoes, especially *Anopheles* spp. by providing refuge from predation. The shorter development period of larvae in wild rice would also expose larvae to predation for a shorter period of time and may partially account for the increased late instar survival.

Kramer & Garcia (1987) showed, in a preliminary laboratory study, that caged gravid *C. tarsalis* laid more eggs in wild rice water than white rice water; however, a repeat of the experiment the following year failed to duplicate these results. Their inconsistent results could have resulted from sampling wild rice water before or after anthesis in their second experiment. The results may also suggest that the laboratory conditions were not appropriate for oviposition by *C. tarsalis*. *Anopheles* spp. were not examined for oviposition preference. Despite the inconclusive results of the oviposition study, the significantly greater number of early instars in wild rice clearly suggest higher oviposition rates in wild rice.

Pollen has long been known to be a nutrient source for a number of arthropods, and extensive studies have been conducted on the honey bee, *Apis mellifera* L., in this regard (Stanley & Linskens 1974). However, little is known about the possible nutrient role of various pollens for mosquitoes. Hopla (1965) referred to a possibility that pollen ingested through nectar by female mosquitoes such as *Aedes communis* (DeGeer) in the Arctic accounted for some egg development; however, to our knowledge, this point has not been experimentally verified. Many plant pollens, fall into the size range (10–100 μm) of particles ingested by larval mosquitoes (Dadd 1971), including wild rice (≈40 μm). It therefore appears that pollens may provide a possible nutrient source.

In the laboratory, *C. tarsalis* larvae developed from second instar to adult when fed with wild rice pollen only. However, the emerged adults were smaller than individuals reared on an laboratory diet, and mortality was greater in the pollen-fed group. Although pollen constituted the primary visible particulate material in the rearing water in these experiments and was readily ingested by the larvae, the microbial contribution to the growth and development of the larvae is unknown. These results suggest that pollen and other flower parts are significant factors in the attraction, oviposition, nutrition, and survival of mosquitoes in wild rice.

Acknowledgments

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