BIONOMICS OF LOUISIANA RICELAND MOSQUITO LARVAE. II. SPATIAL DISPERSION PATTERNS[1]

M. D. ANDIS AND C. L. MEEK[2]

Department of Entomology, Louisiana Agricultural Experiment Station, Louisiana State University
Agricultural Center, Louisiana State University, Baton Rouge, LA 70803

ABSTRACT. A stratified sampling procedure was devised to investigate the spatial patterns of the predominant mosquito species in Louisiana rice fields. Prior to harvest, highly significant differences ($P < 0.01$) in the density of *Psorophora columbiae* larvae existed among strata within the field. Over 93% of the *Ps. columbiae* larvae collected were obtained within 1 m of the contour levees. Following harvest, no significant differences ($P > 0.05$) were detected in the numbers of *Ps. columbiae* larvae collected among strata. Spatial patterns of *Anopheles crucians* larvae were independent of harvest and the larvae were equally distributed among all strata, regardless of collection date.

INTRODUCTION

Very little quantitative information is available concerning the interrelations of mosquito larval population densities and spatial distributions, and their influence upon survey technology. Individuals in a population of mosquito larvae may be distributed within a rice field according to 3 broad patterns: (1) random ($\sigma^2=\mu$), (2) uniform ($\sigma^2<\mu$), or (3) aggregated ($\sigma^2>\mu$) (Southwood 1966, Pielou 1969). As most habitats are not completely homogeneous, it is expected that certain areas will be favored and occupied at the expense of less suitable ones resulting in an aggregated spatial pattern. However, if individuals of a population tend to form groups of a certain size, the distribution of groups may approach randomness.

Determination of the type of larval distribution, the degree of aggregation (if any), and the permanence of groups is necessary if density is to be precisely estimated and an integrated approach to riceland mosquito management is to be effectively monitored. Spatial heterogeneity may significantly influence larval survey technology and, undoubtedly, plays an important role in the outcome of predator-prey interaction. Furthermore, sample methods and statistical analyses which are appropriate for random or uniform larval distribution may be inadequate, misleading, and/or excessively time-consuming when applied to strongly aggregated populations. This paper presents empirical and statistical analyses of the spatial patterns of the predominant rice field mosquitoes in Louisiana.

METHODS AND MATERIALS

The monitoring program was conducted weekly in 25 and 29 ha commercial rice fields of Vermilion Parish, LA during 1980 and 1981, respectively, as previously described by Andis et al. (1983). A stratified sampling procedure was devised to reduce the heterogeneity of the larval rice field mosquito population and to increase the precision of the sample estimates.

Larval samples were collected along 3 equidistant transects that extended the length of each field. Along these transects, 3 ecologically distinct strata were sampled using a 0.1 m² area sampler (Fig. 1). The statistical analyses were based on a model utilizing one field with 3 pans/field, 3 transects/pan, 3 strata/transect and 5 area samples/transect for a total of 45 area samples collected/sample date. The number of individuals collected from each sample was recorded by instar and a standard transformation ($\sqrt{x}$) was performed on the larval captures which normalized the data and permitted the variances of mean catches within and between strata to be calculated. Data from positive collections were then subjected to an analysis of variance using SAS (1982) general linear models procedure for testing the hypothesis that the mean numbers of larvae obtained from each stratum were equal. To obtain additional information on the more detailed nature of the larval

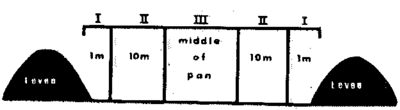

Fig. 1. Habitat strata sampled for assessing population parameters of larval rice field mosquitoes in Louisiana.

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[1] This research was conducted as a cooperative effort between the State Agricultural Experiment Stations of Arkansas, California, Louisiana, Mississippi and Texas and the Agricultural Research Service, USDA as part of the USDA/CRS Southern Regional Projects S–122 on the Biology, Ecology and Management of Riceland Mosquitoes in the Southern Region.

[2] Research Associate and Professor, respectively, Department of Entomology, Louisiana State University, Baton Rouge, LA 70803.

aggregation patterns, estimates of mean crowding ($\overset{*}{X}$) were calculated by the equation $\overset{*}{X}=\overline{X}+(S^2/\overline{X}-1)$ where $\overline{X}$ and S^2 are the sample estimates of mean density and variance, respectively (Lloyd 1967). Since larval distribution patterns are affected by dispersal and mortality of larvae as well as the initial distribution of eggs, estimates of mean crowding ($\overset{*}{X}$) and mean density ($\overline{X}$) were calculated for each larval instar. When mean crowding was plotted against mean density for a given instar, the relation could be fitted to a linear regression and expressed as $\overset{*}{X}=\alpha+\beta\overline{X}$, where α is the intercept on the $\overset{*}{X}$-axis and β is the slope. The intercept and slope are useful indices of the spatial pattern that is characteristic of the species. The index of basic contagion (α) indicates whether a single individual or a positive or negative association of individuals is the basic component of the distribution. The density-contagiousness coefficient (β) suggests how such basic components distribute themselves at different densities (Iwao 1968). The estimation of α and β was made by the usual least squares method and the fitness to the linear regression described by the coefficient of determination (r^2).

RESULTS AND DISCUSSION

The mean densities of each larval instar of *Psorophora columbiae* (Dyar and Knab) and *Anopheles crucians* Wied. are summarized in Tables 1 and 2, respectively. Prior to harvest of the rice field, *An. crucians* was consistently collected at densities significantly greater ($P < 0.05$) than that of *Ps. columbiae*. However, following the post-harvest flood, the mean larval density of *Ps. columbiae* was significantly greater ($P < 0.01$) than the mean larval density of *An. crucians*. Over all 18 sample dates, significantly more ($P < 0.05$) *Ps. columbiae* larvae were collected.

Further analyses indicated that prior to harvest, highly significant differences ($P < 0.01$) in the density of *Ps. columbiae* larvae existed among strata within the field (Table 1). Figure 2 illustrates that prior to harvest, 93.4% of the *Ps. columbiae* larvae collected were obtained from within 1 m of the levees (stratum 1), 6.6% between 1 and 11 m (stratum 2), and no larvae were collected from the middle of the pan (stratum 3). Differences in total numbers of *Ps. columbiae* collected among strata were not attributable to habitat variability. Although there were significant differences in *Ps. columbiae* densities among strata, there were no significant ($P > 0.05$) variations in selected physiochemical parameters of the water among strata (Table 3). Consequently, the abundance of *Ps. columbiae* larvae along the levees may be due, in part, to adult ovipositional behavior as previously reported by Meek and Olson (1976) in Texas ricelands.

Table 1. Temporal and spatial variations in the number of *Psorophora columbiae* larvae per sampling (± S.E.).

Date	Strata	Mean no. larvae[a]				Percent of all instars/stratum[b]
		Instar I	Instar II	Instar III	Instar IV	
18 Mar	1	0.06 (0.06)	0	0	0	100
	2	0	0	0	0	0
	3	0	0	0	0	0
15 May	1	0	0.61 (0.24)	0	0	100
	2	0	0	0	0	0
	3	0	0	0	0	0
6 Jun	1	1.44 (0.53)	2.78 (0.82)	0.17 (0.09)	0.06 (0.06)	81.6
	2	0	1.00 (0.40)	0	0	18.4
	3	0	0	0	0	0
11 Jun	1	0	0	5.11 (0.97)	19.28 (2.74)	92.0
	2	0	0	0	2.11 (0.44)	8.0
	3	0	0	0	0	0
HARVEST						
19 Aug	1	61.36 (23.32)	198.63 (62.14)	0	0	41.2
	2	24.24 (9.35)	217.67 (68.88)	0	0	38.4
	3	82.12 (43.19)	176.00 (79.15)	0	0	20.4
28 Aug	1	22.23 (5.36)	58.81 (13.23)	3.56 (0.76)	0.06 (0.06)	44.7
	2	21.85 (5.19)	42.35 (9.17)	3.50 (0.82)	0.13 (0.09)	35.8
	3	24.63 (8.19)	46.00 (14.20)	3.25 (1.06)	0	19.5
9 Sep	1	0	0	67.25 (13.54)	4.83 (1.01)	35.7
	2	0	0	65.40 (12.77)	3.36 (0.70)	39.7
	3	0	0	65.50 (15.60)	13.13 (2.85)	24.6

[a] Expressed as mean no. larvae/0.1 m^2.

[b] Expressed as percentage of total no. larvae collected/stratum/date.

Table 2. Temporal and spatial variations in the number of *Anopheles crucians* larvae per sampling (± S.E.).

		Mean no. larvae[a]				
Date	Strata	Instar I	Instar II	Instar III	Instar IV	Percent of all instars/stratum[b]
3 Apr	1	0.96 (0.29)	0.89 (0.21)	0	0	44.0
	2	1.16 (0.48)	0.31 (0.17)	0	0	34.7
	3	0.67 (0.19)	1.14 (0.38)	0	0	21.3
10 Apr	1	0.37 (0.14)	0.89 (0.19)	0.48 (0.20)	0	43.7
	2	0.42 (0.17)	0.60 (0.17)	0.44 (0.17)	0	36.6
	3	0.31 (0.14)	1.13 (0.42)	0.14 (0.19)	0	19.7
17 Apr	1	0	0.45 (0.17)	0.86 (0.21)	0.09 (0.09)	30.1
	2	0.33 (0.15)	1.31 (0.52)	0	0.56 (0.21)	48.2
	3	0.55 (0.21)	1.40 (0.34)	0	0	21.7
1 May	1	0	0.86 (0.25)	0	0	25.4
	2	0	1.10 (0.32)	0.92 (0.25)	0	58.7
	3	0	0.64 (0.24)	0.49 (0.26)	0	15.9
7 May	1	0	6.33 (1.90)	0	0	52.8
	2	2.91 (0.51)	1.72 (0.37)	0	0	38.4
	3	0	2.11 (0.57)	0	0	8.8
15 May	1	0	2.72 (0.52)	4.06 (0.69)	0	61.6
	2	0	0.50 (0.13)	1.17 (0.29)	0	15.2
	3	0	1.33 (0.43)	3.78 (1.02)	0	23.2
28 May	1	1.94 (0.34)	2.21 (0.45)	0	0.33 (0.14)	26.4
	2	4.22 (0.67)	3.86 (0.62)	0	0.11 (0.08)	48.4
	3	2.67 (0.66)	3.78 (0.86)	0.78 (0.34)	1.33 (0.46)	25.2
6 Jun	1	0.61 (0.18)	4.72 (0.78)	5.33 (0.85)	3.11 (0.56)	59.9
	2	0.11 (0.08)	2.89 (0.51)	2.50 (0.51)	0	23.9
	3	0	3.56 (0.83)	2.89 (0.83)	1.00 (0.38)	16.2
11 Jun	1	4.17 (0.55)	4.44 (0.74)	1.06 (0.27)	2.11 (0.42)	45.8
	2	0.56 (0.19)	3.39 (0.57)	1.44 (0.34)	1.11 (0.29)	25.3
	3	4.67 (0.98)	4.44 (0.97)	5.67 (1.42)	0.11 (0.11)	28.9
			HARVEST			
19 Aug	1	6.33 (1.27)	1.33 (0.57)	0.17 (0.09)	0	35.6
	2	5.50 (1.41)	0.50 (0.31)	0	0	27.3
	3	14.33 (4.23)	3.00 (1.27)	0	0	37.1
28 Aug	1	0	0	0.44 (0.17)	1.69 (0.38)	38.6
	2	0	0	0.38 (0.15)	1.13 (0.31)	27.3
	3	0	0	0.25 (0.19)	3.50 (0.98)	33.0
9 Sep	1	4.67 (0.73)	0.83 (0.30)	0	0.33 (0.17)	34.3
	2	4.14 (0.75)	1.07 (0.31)	0	0	35.8
	3	6.38 (1.32)	1.13 (0.41)	0	0.13 (0.13)	29.9

[a] Expressed as mean no. larvae/0.1 m^2.

[b] Expressed as percentage of the total no. larvae collected/stratum/date.

Following harvest, the rice field under investigation was reflooded for the cultivation of a second crop of rice. Equipment ruts from harvesting operations created a new series of *Ps. columbiae* oviposition sites within the rice field (Meek and Olson 1976, 1977; Olson and Meek 1977, 1980). Consequently, no significant differences ($P > 0.05$) existed in the numbers of *Ps. columbiae* larvae collected among dates or strata following the post-harvest flood (Table 1).

These spatial data alone indicate that more efficient and precise larval sampling strategies can be devised for the detection and surveillance of *Ps. columbiae* populations. From the data described herein, mosquito control per-

Table 3. Spatial variation among selected environmental parameters, expressed as mean values (± S.E.)[a]

Strata	Water temperature	pH	Conductivity	Water depth	Dissolved oxygen
1	31.5 (2.2)	7.1 (0.4)	26.7 (9.8)	10.6 (4.1)	10.7 (1.1)
2	29.6 (2.1)	6.3 (0.3)	23.5 (8.6)	10.9 (4.5)	10.0 (0.7)
3	30.4 (2.0)	6.7 (0.3)	21.8 (7.9)	11.2 (3.8)	10.5 (0.9)

[a] No significant difference ($p > 0.05$) existed in mean values among strata.

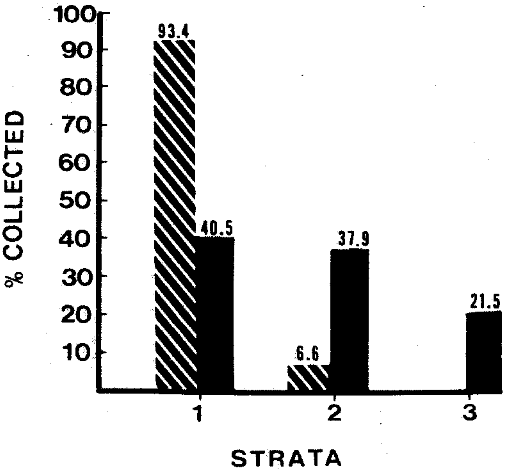

Fig. 2. Percent distribution of the number of *Psorophora columbiae* larvae collected among strata prior to harvest (cross-hatch) and post-harvest (solid bar).

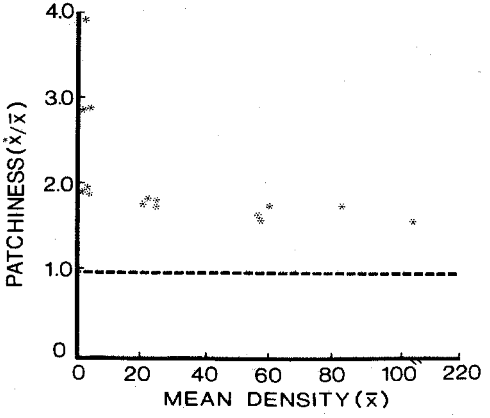

Fig. 3. Relationship between patchiness and the number of *Psorophora columbiae* larvae collected/0.1 m^2 area sample.

sonnel could best utilize their time and efforts by sampling only along the contouring rice field levees. Following harvest, when equipment ruts are prevalent, all strata within the pan become equally important in the production of *Ps. columbiae* larvae. Given that the distribution of larvae within the pan is known, it is statistically acceptable and operationally feasible to again randomly sample only along the levees, regardless of collection date. This procedure should prove to be more cost efficient than current sampling strategies, enable mosquito control/research personnel to make precise density estimates which are comparable among studies, and prevent farmer complaints concerning rice destruction from within field sampling.

The distribution of *Ps. columbiae* larvae within strata was consistently patchy (Fig. 3). A patchiness of unity indicates an approximately random distribution; mutual repulsion would be indicated by a value below unity. To obtain more detailed information regarding the larval aggregation patterns within strata, estimates of mean crowding ($\overset{*}{X}$) were calculated for the data collected on each sample date (Lloyd 1967). When the $\overset{*}{X}$'s were plotted against $\overline{X}$'s for each instar, the relation was fitted to a linear regression. The results for each larval instar are shown by the estimated values of α and β in Table 4. The fact that the values of α were greater than zero suggests that the larvae had a tendency to occur in groups, especially instars I and II, which was undoubtedly related to the female ovipositing in mass rather than depositing single eggs in the soil at random. As the values of β were larger than unity, these groups of larvae were aggregated within strata. It should be noted that the changes in the distribution pattern from early to late instars are reflected in α and β values of these regressions. The decrease in α may indicate the typical pattern of reduction in larval numbers both by dispersal and by the action of mortality factors. The decrease of β values for early and late instars may suggest density dependence of the process of dispersal and the operation of mortality factors during this time interval. Due to this disparity between the $\overset{*}{X}-\overline{X}$ regression values for early and late instars and the previously reported differences in larval instar relationships (Andis et al. 1983), the spatial structure of larval *Ps. columbiae* populations can best be described by distinguishing individuals of developmental stages I and II (early) from developmental stages III and IV (late). The $X-\overline{X}$ relationships for the early and the late instar *Ps. columbiae* larvae are similar for each sampling date and strata. Thus, there were no

Table 4. The values of α and β in the $\overset{*}{X}$-$\overline{X}$ regression for the distribution of each *Psoropora columbiae* instar.

Instar	α	β	r^2
1	1.30	1.92	0.97
2	1.10	1.68	0.95
3	0.13	1.51	0.94
4	0.09	1.31	0.89

essential differences among the spatial patterns within the field over the period of sampling. Consequently, all the data collected at different times and strata were plotted to obtain general $\overset{*}{X}-\overline{X}$ relationships for early and late developmental stages. The resulting relationships are illustrated in Fig. 4 and can be fitted by the linear regressions $\overset{*}{X}=1.2 + 1.8\ \overline{X}$ ($r^2=0.97$) and $\overset{*}{X}=0.11 + 1.4\ \overline{X}$ ($r^2=0.92$ for early and late instar *Ps. columbiae,* respectively.

The spatial patterns of *An. crucians*, unlike *Ps. columbiae,* were independent of harvest (Table 2) and the larvae were equally distributed among all strata, regardless of collection date (Fig. 5). These data indicated that there was no gain in precision from stratification, yet sampling within 1 m of the rice field levees would provide a reliable and economically feasible index to the abundance of larval populations when used in conjunction with *Ps. columbiae* surveillance.

The spatial structure of the *An. crucians* larval population within the field, analyzed by the $\overset{*}{X}-\overline{X}$ regression method, indicated that the basic component of the larval distribution was not a group of individuals but a single individual and such components were distributed contagiously over the field (Fig. 6). This basic pattern did not change significantly according to developmental stage, sample data or stratum. Therefore, the distribution pattern of the *An. crucians* population in a rice field was described by the single linear regression, $\overset{*}{X}=0.01+1.19\overline{X}$ ($r^2=0.90$).

Studies on spatial distribution of rice field mosquito larvae will establish a statistical basis for interpreting field data and designing appropriate sampling schemes. Using the methods and techniques described by Andis et al. (1983) and the information on the dispersion patterns, a foundation has been laid for the development of a more efficient and precise strategy for sampling rice field mosquito larvae.

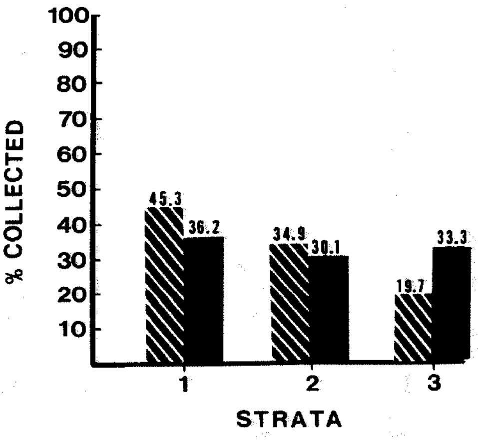

Fig. 5. Percent distribution of the number of *Anopheles crucians* larvae collected among strata prior to harvest (cross-hatch) and post-harvest (solid bar).

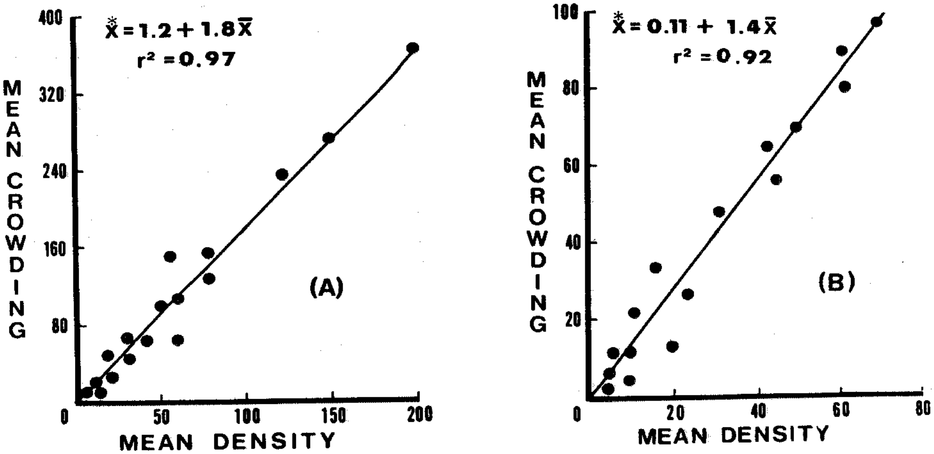

Fig. 4. Relationship between mean crowding and mean density (no./0.1 m^2) for the distribution of *Psorophora columbiae* larvae within strata. (A) LI and LII (B) LIII and LIV.

Consideration may now be given to the determination of optimum sample sizes based on the desired level of precision and the applica-

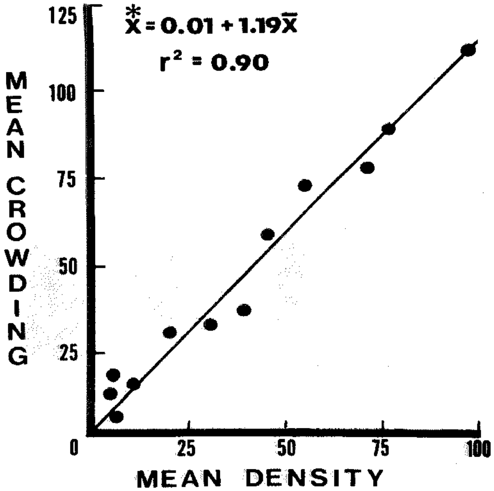

Fig. 6. Relationship between mean crowding and mean density (no./0.1 m^2) for the distribution of *Anopheles crucians* larvae within strata.

tion of sequential methods to precisely estimate population density as well as to classify population levels in relation to a predetermined threshold.

ACKNOWLEDGMENTS

The authors wish to express their grateful appreciation to the personnel of the Vermilion Parish Mosquito Control District for their assistance and cooperation throughout this study. Special thanks are extended to Louisette Leonard for her technical assistance, Ismelda Hyland for typing the manuscript, and the National Institutes of Health PROPHET system for aid in data management, numerical computation, and interactive graphics.

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