PARITY, FECUNDITY AND BODY SIZE OF *MANSONIA DYARI* IN FLORIDA

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ABSTRACT. Seasonal trends in reproductive performance and size were examined among female *Mansonia dyari*. The incidence of parity ranged between 6.9 and 58.1% and averaged 22.5% during an 8-month interval, with 4 peaks in parous rate believed to follow periods of emergence. Parous rates were positively correlated with wing lengths, indicating size-dependent survivorship. Wing lengths were highest in the winter and early spring, decreased to a minimum at the end of summer, and increased in the autumn, showing negative correlations with ambient temperatures recorded prior to adult capture. Female biomasses and fecundities were positively correlated with wing lengths, and their mean values varied significantly among sample dates. Egg development in *Ma. dyari* was completed by 5.4 days post blood meal at 26°C and 7.6 days at 20°C. No evidence for autogeny was observed.

INTRODUCTION

As important vectors of human filariae in the Afrotropical and Oriental regions, mosquitoes of the genus *Mansonia* (*Mansonioides*) have been objects of comprehensive entomological studies (e.g, Laurence 1960, Wharton 1962). Neotropical *Mansonia* (*s.s.*), all of which belong to the subgenus *Mansonia*, include 12 species (Knight and Stone 1977; Knight 1978), of which two, *Ma. dyari* Belkin, Heinemann and Page and *Ma. titillans* (Walker), range into Florida. Although *Ma. dyari* has been identified as a maintenance vector of St. Louis encephalitis (SLE) virus in Panama (Gorgas Memorial Laboratory 1978), and *Ma. titillans* has been incriminated in the transmission of Venezuelan equine encephalitis virus to man in the Caribbean (Gilyard 1944), relatively little is known of the life histories of these 2 species.

Investigations of the habits of *Ma. dyari* in Florida (referred to in earlier literature as *Ma. indubitans* Dyar and Shannon) have, until recently, been limited to studies on voltinism, seasonality and preferred host plants (Provost 1976, Lounibos and Escher 1985, Slaff and Haefner 1985). In spite of prolific local abundance of *Ma. dyari* in the vicinity of its primary host plant, water lettuce (Lounibos and Escher, 1985), there is no published information on the reproductive ecology of this species. Such information would be important if *Ma. dyari* should play a role in the maintenance of SLE virus, a human health concern in Florida.

MATERIALS AND METHODS

Collection sites: Adult *Ma. dyari* were collected by methods described below at Chinese Farm in subtropical St. Lucie County (27° 30′N, 80° 30′W) and separated from related species by diagnostic keys. This collection site harbors abundant water lettuce (*Pistia stratiotes* Linn.) growing in abandoned aquaculture ponds. Water lettuce occurs year-round at Chinese Farm, although large plants typically die back during winter cold, resulting in a depression of plant biomass in the late winter and spring (DeWald and Lounibos 1990). A thermograph situated 1 m above ground in an oak-palm woodland 6 km to the north of Chinese Farm provided continuous records of ambient temperatures for the study. The central tendency of weekly temperature was calculated as weekly (maximum + minimum)/2, hereinafter referred to as the weekly temperature.

Parity: Parity was scored by examination of tracheolar skeins of freshly killed individuals captured with dry ice-baited CDC traps operated from dusk to dawn. Four collections for parity determination were made between September 1986 and February 1987, then 18 successive collections at approximately fortnightly intervals from April to December 1987. Ovaries of 25 to 39 females were examined from each collection except for December 1986 when only 20 individuals were scored. Females with mature eggs or undigested blood were excluded.

Wing lengths and biomasses: Wing length was measured from the base of the costa to the wing margin, exclusive of fringes, under 20×. From 3 separate CDC light trap collections in June, August and October of 1987, a wing was removed and measured, and the remaining corpse dried at 80°C for 24 h. Dry weights were measured to the nearest 0.01 mg on a Cahn electrobalance.

Egg development time: During August 1987, females were collected in 'lard-can' traps in which they were allowed to blood-feed from a chicken. On the morning of the day of collection, females with blood were placed in incubators at 12L:12D and 26 ± 1°C or 20 ± 0.5°C. Mosquitoes were held in 0.045 m^3 cages with access to a 10% sucrose solution. At successive 24-h intervals beginning 62 h after blood-feeding at 26°C and 86 h at 20°C, 10 females were dissected to assess

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ovarian development. Christophers' (1911) ovarian stages (I–V) were transcribed into arabic numerals. Intermediate stages of 2.5, 3.5 and 4.5, corresponding respectively to ovarian stages IIb, IIIb and IVb of Clements (1963), were recognized. Follicles in which all but the anterior tube of the mature egg (Linley et al. 1986) were filled with yolk were scored as 4.5.

Fecundity: On 8 dates between April and November 1987, *Ma. dyari* females were captured in dry ice-baited CDC or chicken-baited 'lard can' traps and allowed to blood-feed on chickens. Females with blood were held at 26 ± 1°C, 12L:12D with access to 10% sucrose but no oviposition site. Six to 10 days after the blood meal, the length of a wing was measured, the female was killed and the number of mature eggs (stage 5.0 follicles) counted under a dissecting microscope.

Autogeny: Females were captured with emergence traps (Slaff et al. 1984) placed over water lettuce, then maintained with males for 7–10 days in 0.045 m^3 cages at 26°C in a 12L:12D incubator or outside in the shade in ambient summer conditions. Subsequent examination of spermathecae revealed that insemination, which is necessary for the expression of autogeny in some mosquito species (O'Meara 1985), was not occurring under these conditions. Therefore, females from 2 autumnal collections were exposed to males in 2.5 × 1 × 1 m outdoor cages, where insemination rates of 34.3% ($n = 35$) and 73.9% ($n = 23$) were recorded. The ovaries of all dissected females were staged by Christophers' (1911) method.

RESULTS

Trends in parity and wing length: The incidence of parity varied over time, ranging between 6.9% in late February to 58.1% in late May (Fig. 1). Overall, 21.9% of all females dissected ($n = 668$) between September 1986 and December 1987 were parous. Between February and December 1987, representing most of one annual cycle, 22.5% of females ($n = 583$) were parous. During this period, 4 peaks in parity were recognized in late May, mid-July, early September and mid-December.

Mean wing lengths were greatest in early spring, declined, on average, during the summer and were shortest in early September (Fig. 2). Wing lengths increased again in the autumn, but average values in November and December were less than in the preceding spring. Average wing lengths from 19 collection dates were negatively correlated with weekly ambient temperatures, which ranged from 13.5 to 26°C. Significant correlations were obtained with temperatures which lagged adult capture by 3–15 weeks (Table 1). Testing for homogeneity among all correlation coefficients (Sokal and Rohlf 1981), revealed that the *r*s could have come from the same population ($\chi^2 = 5.696 < \chi^2_{.05\,[7]} = 14.067$).

The mean ± SD wing length of all parous females (3.23 ± 0.25 mm, $n = 131$) was not significantly different ($t = 1.38$, $P = 0.16$) from that of all nulliparous females (3.20 ± 0.24 mm, $n = 452$). Comparisons were performed separately for each collection date to test the null hypothesis (two-tailed) that the mean wing length of parous females was equal to that of nullipars. Once in early May and once in late July, mean wing lengths of parous mosquitoes were significantly longer (May: $t = 2.74$, $P = 0.01$; July: $t = 2.24$, $P = 0.03$) (Fig. 2). For a single collection in mid-June, the mean wing length of nulliparous individuals was signifi-

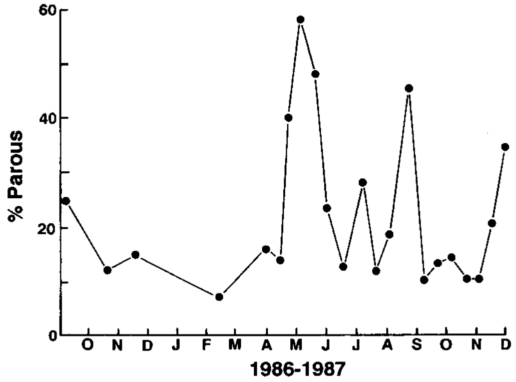

Fig. 1. Frequency of parity among *Mansonia dyari* captured by CDC traps at Chinese Farm. The first 4 samples were not separated by regular intervals, but between April and December 1987; sampling was done fortnightly; $n = 25$–39/point except for December 1986 where $n = 20$.

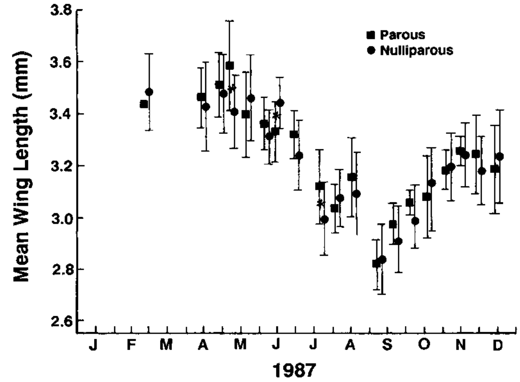

Fig. 2. The wing lengths of *Mansonia dyari* females dissected for parity on 19 occasions during 1987. Vertical bars represent ± 1 SD. Means separated by asterisks were significantly different as determined by *t*-tests (two-tailed).

Table 1. Product-moment correlations between weekly ambient temperatures [(maximum + minimum)/2] and mean wing lengths of *Mansonia dyari.*

Time lag (weeks)	1	3	5	7	9	11	13	15
r[1]	−0.18	−0.46	−0.68	−0.70	−0.76	−0.62	−0.61	−0.61

[1] Levels of significance for 17 df: $P_{.01} = 0.58$; $P_{.05} = 0.46$.

Table 2. Regression and ANCOVA results for biomass regressed upon wing length and *a posteriori* comparison of adjusted means.

	Regression[1]				ANCOVA[2]		
Sample date	*n*	*b*	*a*	R^2	Mean mass (mg)	Adjusted mean	S.E.
June	67	0.006	−1.586	0.581	0.569	0.417a	0.013
Aug.	80	0.005	−0.975	0.583	0.401	0.436a	0.008
Oct.	80	0.006	−1.116	0.448	0.560	0.625b	0.010

[1] Coefficients in the equation $y = bx + a$; all R^2 values significant at $P < 0.001$.

[2] Adjusted means followed by different letters are significantly different at $P < 0.05$ [approximate interval method of Gabriel (1978)].

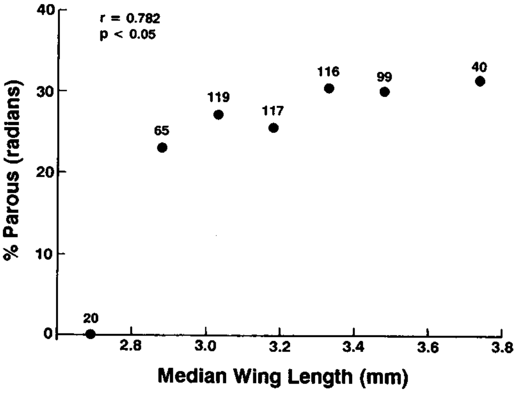

Fig. 3. The relationship between parous rate and median wing length of 7 size classes of *Mansonia dyari.* Numbers above each point are sample sizes. The vertical scale converts rates into the angular transformation.

Table 3. ANCOVA results for fecundity regressed upon wing length and *a posteriori* comparison of adjusted means.

Sample date	n	Mean no. eggs	Adjusted mean[1]	S.E.
April 13–14	16	152.8	136.9 ab	8.53
April 27–28	10	154.6	137.2 ab	10.34
May 20–21	9	122.7	107.7 a	10.38
June 8–9	6	159.5	143.2 ab	12.44
July 22–23	7	158.1	167.4 b	10.90
August 4–5	33	136.7	144.4 ab	5.40
Sept. 29–30	25	145.3	158.3 b	6.87
Nov. 18–19	17	154.3	155.4 b	6.76

[1] Adjusted means which do not share a common letter are significantly different at $P < 0.05$ [approximate interval method of Gabriel (1978)].

cantly longer than their parous counterparts ($t = 2.62$, $P = 0.01$). From the 16 remaining comparisons there was no evidence to reject the null hypothesis of equal wing lengths ($0.21 < P < 0.92$).

Data from the above 19 collection dates were pooled and females segregated into 7 wing length classes. The size classes were 0.15 mm in width except for the smallest, which ranged from 2.59–2.79 mm and the largest, ranging between 3.56 - 3.92 mm. Parous rates, subjected to the arcsin transform, were positively correlated with median wing lengths of the 7 size classes (Fig. 3). No parous individuals were recorded amongst the smallest *Ma. dyari.*

Wing lengths and body mass: Plots of dry weight versus wing length for 3 sample dates yielded significant linear regressions accounting for 45–58% of the explained variance (Table 2). The three regression coefficients did not differ significantly from one another ($F_{2,221} = 2.738$, $P = 0.067$), indicating homogeneity of slopes.

Mean dry weights from the 3 sample dates were compared following analysis of covariance (ANCOVA) which adjusted for differences in wing lengths among the samples. The ANCOVA detected significant differences among adjusted mean biomasses ($F_{2,221} = 165.836$, $P < 0.001$). An *a posteriori* comparison indicated that October's adjusted mean dry weight was significantly greater than June's or August's (Table 2).

Fecundity: Variation in number of eggs was high, ranging from 66 to 209. Three females with no eggs were discounted from further analyses. Mean numbers of eggs per sample varied from a low of 122.7 in May to a high of 159.5 in June, but showed no obvious seasonal trends (Table 3).

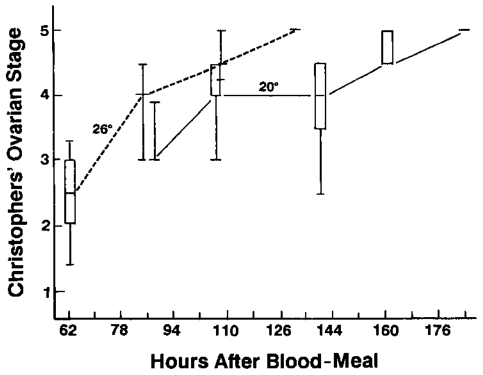

Fig. 4. Box plot of Christophers' stage of ovarian development as a function of time. Broken line connects median (50th percentile) values at 26°C, and solid line connects medians at 20°C. Upper and lower boundaries of boxes are 75th and 25th percentiles, and upper and lower bounds of stems are 90th and 10th, respectively. Where absent, these percentiles were identical to the more central values. Each point based on 10 dissected females except at 62 h ($n = 9$) and 86 h ($n = 7$) post blood meal.

The regression of fecundity on wing length was significant ($F_{1,121} = 6.408$, $P = 0.013$), but explained only 5% of the variance. When regression coefficients were compared among sample dates, no significant differences were detected ($F_{7,114} = 0.451$, $P = 0.867$). An ANCOVA with wing length as the covariate showed significant variation among the adjusted mean fecundities ($F_{7,114} = 2.900$, $P < 0.001$). Computation of the 95% confidence intervals of adjusted means indicated that significantly fewer eggs were developed in May than in samples from July, September or November (Table 3).

Gonotrophic cycle lengths: Dissections after blood meals revealed that egg development was complete (stage 5.0) for all females at 183 h (7.6 days) post blood meal at 20°C and 129 h (5.4 days) at 26°C (Fig. 4). Although the median female at 20°C had developed ovaries to stage 4.0 by ca. 4 days post blood meal, completion of the final stage by all individuals required another 3 days at the lower temperature. Detection of a few resting stage (2.0) follicles between 62 and 139 h (Fig. 4) indicated that blood had not promptly triggered egg development in all females.

Absence of autogeny: Dissected ovaries of all but 1 of 169 females held without blood for 9–15 days after emergence were in Christophers' stage 1.0 or 2.0. The lone exception had one-third of her follicles developed to stage 3.0. These observations indicated that neither mated nor unmated *Ma. dyari* are able to complete egg development autogenously.

DISCUSSION

The 4 peaks in parous rates during 1987 presumably followed periods of *Ma. dyari* emergence. Among most temperate mosquito species, the frequency of parity is low while adult numbers increase, then rises after the emergence peak (Morris and DeFoliart 1971). In Florida *Ma. dyari* is multivoltine, the number and timing of generations depending on winter temperatures that affect water lettuce abundance (Provost 1976, Lounibos and Escher 1985). Hibernal dieback of *P. stratiotes* was not severe in 1986–87 (DeWald and Lounibos 1990), allowing a spring emergence of *Ma. dyari*, a high proportion of which blood-fed and oviposited in May (Fig. 1).

Among *Mansonia uniformis* (Theobald) in Ceylon, a parous rate of 50–60% was found to be relatively constant from month to month (Samarawickrema 1968). In equitable, equatorial temperatures the gonotrophic cycle of *Ma. uniformis* remains close to 4 days, and 1 blood meal is sufficient to mature eggs (Wharton 1962). Under such conditions daily survival may be realistically estimated by the parous rate formula of Davidson (1954).

Steady-state conditions do not apply to *Ma. dyari* populations in Florida where the parous rate underwent frequent large fluctuations (Fig. 1), and adult mosquitoes may experience average temperature differences of >10° between summer and autumn, which will affect gonotrophic cycle length (Fig. 4). Nevertheless, if the period of sampling between February and December represents a complete breeding season, then the overall parous rate (0.225) is the annual probability of completing one gonotrophic cycle (Hawley 1985).

Size variation within natural mosquito populations has been hypothesized to be related to larval resource limitations or predation (Fish 1985). Fish calculated coefficients of variation (CVs) to compare the variability in size of 10 species of northern mosquitoes captured in light traps. Using the same common regression equation for converting wing lengths to biomasses, we have calculated a CV for *Ma. dyari* of 23.59. This places *Ma. dyari* in Fish's category of moderate size variability, composed mainly of mosquito inhabitants of permanent marshes and lake margins where predation is considered the most important determinant of invertebrate community structure (Zaret 1980). Although attachment to roots may protect *Mansonia* larvae and pupae from some predators (Van den Assem 1958), fish and Odonata larvae consume *Ma. dyari* immatures on water lettuce in Florida (L. P. Lounibos, unpublished data).

Seasonal samples often show an inverse relationship between correlates of body size and environmental temperature (Landry et al. 1988, Bock and Milby 1981). Wing lengths of *Culex tarsalis* Coquillett in central California showed a high negative correlation with ambient temperature one week before trapping (Bock and Milby 1981). For *Ma. dyari* temperature lags of 3 or more weeks before capture yielded higher correlations with wing lengths (Table 1). These different temporal relationships to ambient temperature may reflect both the slower larval growth of *Mansonia,* requiring almost 1 month from hatch to emergence under optimal conditions for *Ma. uniformis* (Laurence 1960), and the slower warming of the deeper, shaded larval habitats of *Ma. dyari.*

Although a few studies have indicated that large mosquitoes of some species or populations may be more likely than smaller counterparts to be parous (Haramis 1983, Packer and Corbet 1989), other investigations have revealed no relationship between body size and survival, as measured by frequency of parity or recapture (Landry et al. 1988, Walker et al. 1987). Our data indicate that larger *Ma. dyari* are more likely to be parous, the smallest females rarely completing a gonotrophic cycle (Fig. 3). This evidence supports the presence of size-dependent survivorship among *Ma. dyari.*

Females from October samples had a significantly higher adjusted mean biomass than samples from June or August (Table 2). Van den Heuvel (1963) demonstrated that the relationship between dry body weight and wing length among *Aedes aegypti* (Linn.) depended upon the temperature experienced by developing larvae. The seasonal differences in *Ma. dyari* biomass may be related to temperature changes in the larval habitat.

Autogeny has never been reported in the genus *Mansonia* (O'Meara 1985), although probably few species have been examined. *Ma. dyari* apparently require blood to develop eggs. There is no information on blood meal sources of *Ma. dyari* in Florida, but this species feeds on mammals and birds in Panama (Gorgas Memorial Laboratory 1978), where cormorants and herons are suspected as reservoirs of SLE virus (J. L. Petersen, personal communication). Birds which frequent water lettuce habitats may also provide blood sources for *Ma. dyari* in Florida.

Although fecundity was positively related to wing length, the regression explained a small proportion of variance compared to similar fecundity:size relationships calculated for tree hole *Aedes* (Livdahl 1984, Hawley 1985). Both biological and methodological factors may contribute to this difference. In *Aedes sierrensis* (Ludlow) and probably also *Aedes triseriatus* (Say), variations in adult size are important population regulating mechanisms (Hawley 1985). Size variability is less among *Ma. dyari* and, hence, probably less important in population regulation. Secondly, in contrast to Livdahl's and Hawley's work, our study controlled neither female age nor blood meal size, which factors among other culicid species contribute to the large deviations from comparable regressions (Packer and Corbet 1989).

The average number of eggs developed by field-caught *Ma. dyari* ranged between 122 and 159 (Table 3), which is more than the mean numbers of 101 and 111 matured by laboratory-reared *Ma. uniformis* or *Ma. africana* (Theobald), respectively (Laurence 1960). The differences between mean fecundities adjusted for wing length (Table 3) might be explained by discrepancies in mosquito ages. The significantly lower fecundity value occurred in late May when the parous rate was highest (Fig. 1). Since mosquito clutch size tends to decrease in successive gonotrophic cycles (Clements 1963), the older age structure of the May *Ma. dyari* sample may have contributed to its decreased average fecundity.

Knowing the annual probability (P) of a female's completing a gonotrophic cycle, then the number of egg clutches laid per female is given by $P/1 - P$ (Hawley 1985). For *Ma. dyari* this value is 0.29. Based on the range of fecundities of 122–159, the average female will contribute 35–46 eggs to the next generation.

ACKNOWLEDGMENTS

We appreciate the help of L. B. DeWald and R. L. Escher in the field. Comments from J. F. Day, G. F. O'Meara and, particularly, W. A. Hawley aided manuscript preparation. The research was supported, in part, by contracts from the U.S. Army (DAMD 17-85-C-5182) and Florida Department of Health and Rehabilitative Services. This is University of Florida IFAS journal series no. R-00147.

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