

**Blood-feeding and Capacity for Increase in the Pitcher-plant Mosquito,
*Wyeomyia smithii*¹**

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ABSTRACT

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Northern *Wyeomyia smithii* (Coquillett) (Diptera: Culicidae) are obligatorily autogenous; southern *W. smithii*, although capable of autogenous development, may consume a blood meal. The clutch of eggs resulting from a blood meal contributes little to capacity for increase. Capacity for increase is inversely correlated with mean crowding of the overwintering population. These results suggest that the principal role of hematophagy in *W. smithii* relates to increasing the contribution to total reproductive effort made by the 2nd and subsequent ovarian cycles.

The mosquito, *Wyeomyia smithii*, oviposits and completes its immature development only within the leaves of the purple pitcher plant, *Sarracenia purpurea* from the Gulf Coast (ca. 30° N latitude) to Labrador and northern Saskatchewan (ca. 54° N latitude) (Bradshaw and Lounibos 1977). Throughout this range, *W. smithii* overwinter as larvae in a photoperiodically initiated and maintained state of dormancy or diapause (Smith and Brust 1971, Bradshaw and Lounibos 1972, 1977, Evans and Brust 1972). Censuses of the overwintering larvae are therefore representative of the population as a whole since there are no other surviving stages of the life cycle. Furthermore, the discrete nature of this mosquito's habitat simplifies estimates of density or crowding.

Little is known about the life-history tactics of *W. smithii*. Northern *W. smithii* are autogenous (do not require a blood meal for ovarian maturation) and although apparently equipped for blood feeding (Hudson 1970), they are not known to suck blood (Smith 1940, Smith and Brust 1971). Smith and Brust (1971) describe autogeny among *W. smithii* from Canada and North Carolina. Bradshaw and Lounibos (1977) were able to rear *W. smithii* from the Gulf Coast as well as low elevations in North Carolina without blood feeding. However, I personally have been fed upon by *W. smithii* while doing field studies, both at low elevations in North Carolina and along the Gulf Coast. Moreover, I have observed *W. smithii* taking blood from the eastern box turtle, *Terrepenne carolina* (L.), in north Florida. In the laboratory, I have confirmed hematophagy among *W. smithii* from low elevations in North Carolina and from along the Gulf Coast. In the present paper, I describe the consequence of hematophagy on capacity for increase among laboratory populations and relate capacity for increase to mean crowding among the overwintering population.

Materials and Methods

I obtained overwintering larvae of *W. smithii* from Liberty and Santa Rosa Co., FL, Brunswick and Moore Co., NC, and Ocean Co., N.J. during Jan., 1976. I selected only plants with undamaged, intact leaves, clipped each leaf off, split it open, and flushed out the contents. I sampled only the 1975 crop of leaves since these are the leaves in which *W. smithii* prefer to oviposit (Istock

et al. 1976, Fish and Hall 1978). To estimate density factors impinging upon individuals in a population, one needs to know not the number of organisms in the mean habitat (mean density) but rather the number of other organisms an individual encounters on the average (mean crowding). Consequently, I censused the number of living larvae in each leaf and, treating leaves as discrete habitats, calculated the mean crowding (m^*) for each location as described by Lloyd (1967):

$$m^* = \frac{\sum \{ (n_i - 1) (n_i) \}}{\sum n_i}$$

where n_i is the number of individuals in the i th leaf.

The intrinsic rate of increase, r , is a fundamental parameter of fitness for any population. The rate, r , is defined by

$$\sum l_x m_x e^{-rx} = 1 \quad (1)$$

where l_x and m_x are the probabilities of individual survivorship to and reproductive effort at age x (Andrewartha and Birch 1954, Crovello and Hacker 1972). Equation (1) does not readily relate r to other population or life-history parameters and many investigators approximate r by r_c , capacity for increase (Laughlin 1965, Southwood et al. 1974), defined by

$$r_c = \frac{\ln(R_0)}{MGT} \quad (2)$$

where R_0 is the replacement rate per individual and MGT is the mean generation time. To determine r_c , I allowed *W. smithii* from various localities to mate in a 0.2-m² cage and oviposit into a pitcher plant. I then collected 100-140 eggs, all oviposited over a 24-h period as the uniform aged parental cohort. I reared members of the parental cohort to pupation in 100 mm culture dishes on long days (L:D = 16:8) and a daily temperature cycle of 32°:25°C = 16:8 h. I transferred the pupae to mating cages where they ecdysed and immediately had access to a pitcher-plant. I changed the plant every 3-5 days and tallied the number of F_1 eggs therein. Then,

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$$R_0 = \frac{\sum E_x}{E_p}$$

where E_p is the number of eggs in the parental cohort and E_x is the number of F_1 eggs oviposited at time x in days from the day of oviposition of the parental cohort,

$$MGT = \frac{\sum xE_x}{\sum E_x}$$

and r_c is found by using Equation (2). Generation time may be divided into 2 components: pre-adult development (days from day of oviposition to day of adult ecdysis) and reproductive lag (days from adult ecdysis to oviposition). I calculated mean pre-adult development time (A) by

$$A = \frac{\sum xEcl_x}{\sum Ecl_x}$$

where Ecl_x is the number of adults eclosing on day x ; reproductive lag (RL) is then given by

$$RL = MGT - A$$

Larval food consisted of a 3:1 mixture by volume of ground guinea pig chow and freeze-dried brine shrimp (*Artemia salina*). I fed the larvae 2-3 times/week at a level sufficient to prevent total consumption of food but below that which would foul the water. I provided adults

with a cotton wad soaked in molasses to which I had added 2 ml/liter absolute ethanol saturated with para amino hydroxybenzoate as mold inhibitor.

Results

In the absence of blood meals, oviposition occurred over a brief period so that F_1 eggs per parental cohort egg (R_0) increased rapidly as a function of time and then leveled off (Fig. 1). Capacity for increase was highest for the North Carolina population and lowest for the Florida population (Table 1). Higher capacity for increase among the North Carolina population resulted both from a greater replacement rate and significantly shorter generation time. Since there was no significant difference between the pre-adult period of these two populations (Table 1), the increase in generation time in Florida is probably due to the increased reproductive lag.

To determine what contribution a 2nd, anautogenous (blood feeding) ovarian cycle would make to capacity for increase, I reared a North Carolina and a Florida population and allowed them to oviposit as before. The above experiment (Fig. 1) showed that the replacement rate function leveled off by day 35, suggesting that the ovaries of the parental population had been depleted by that time. I then offered the Florida population a blood meal (human) on day 35 and the North Carolina population a blood meal on day 40 after an additional 5 day lag. Eight females fed on each occasion (Fig. 1) and an increase in egg production followed shortly thereafter. As before, the population from North Carolina had a

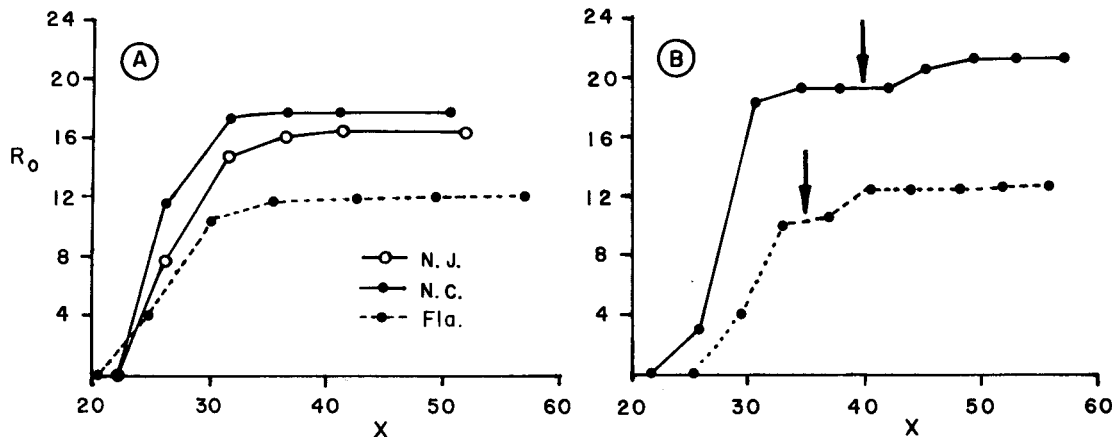


FIG. 1.—Trajectories of replacement rate (R_0 = number of F_1 eggs per egg in the parental cohort) over age (x) of the parental cohort. (A) Populations denied blood meals; (B) populations offered a blood meal (human) at times indicated by the arrows. Eight females fed on each occasion.

Table 1.—Life-history traits of *W. smithii* from Florida (Santa Rosa Co.), North Carolina (Brunswick Co.), and New Jersey when denied blood meals. One-way analysis of variance revealed significant differences among localities for both generation time ($F_{2,5825} = 132$; $P < 0.001$) and pre-adult development ($F_{2,315} = 7.4$; $P < 0.01$).

Origin	E_0^*	%Ecl*	R_0	MGT	r_c	A	RL
FL	128	82	12.31	29.8a**	0.084	24.7a	5.2
NC	127	87	17.89	28.1	0.103	24.2a	3.8
NJ	120	86	16.50	29.6a	0.095	26.3	3.3

* E_0 , number of eggs in parental cohort; %Ecl, percent of E_0 eclosing as adults
 ** numbers followed by the same letter are not significantly different ($P > 0.05$); all others are highly significantly different ($P < 0.01$) by Duncan's Multiple Range Test.

Table 2.—Life history traits of *W. smithii* from Florida (Liberty Co.) and North Carolina (Moore Co.) before (a) and after (b) an opportunity to obtain a blood meal. One way analysis of variance revealed significant differences among localities in generation time ($F_{1,3863} = 575$; $P < 0.001$) but not pre-adult development ($F_{1,182} = 1.28$; $P > 0.05$).

origin	E_0	%Ecl	(a) on day 35					(b) on day 50		
			R_0	MGT	r_c	A	RL	R_0	MGT	r_c
NC	138	69	19.36	29.9	0.099	25.9	4.0	21.25	31.4	0.097
FL	115	100	10.47	31.7	0.074	26.2	5.5	12.73	33.6	0.076

higher capacity for increase due to a greater replacement rate and slower generation time; again, there was no difference between the pre-adult periods of the 2 populations and the increase in generation time may be attributed to reproductive lag (Table 2). Within each population, eggs following hematophagy resulted in greater capacity for increase only among the Florida mosquitoes. Even if the mean generation time for the North Carolina population is adjusted by subtracting 5 days from x for egg production after the blood meal, there is still no increase in r_c (r_c with x adjusted 5 days downward = 0.099).

Capacity for increase was highly correlated with mean crowding among the overwintering population at the locality of origin (Fig. 2).

Discussion

W. smithii from higher latitudes or altitudes are all autogenous; at low elevations in North Carolina or along the Gulf Coast, they are capable of autogenous development but may also feed on blood. Of those individuals which take a blood meal, the 2nd clutch of eggs makes a positive contribution to capacity for increase only if it is produced shortly after the 1st clutch (Table 2). These results do not show what contribution blood-feeding makes to capacity for increase when the opportunity for a blood meal exists throughout adult life. Lea (1964) found that reduced larval nutrition in an autogenous strain of *Aedes taeniorhynchus* lowered the incidence of autogeny among the resulting adults. *W. smithii* in the present study encountered abundant resources as larvae in the laboratory. Under natural conditions, resources may be less abundant and southern *W. smithii* may then consume blood for the first ovarian cycle as well.

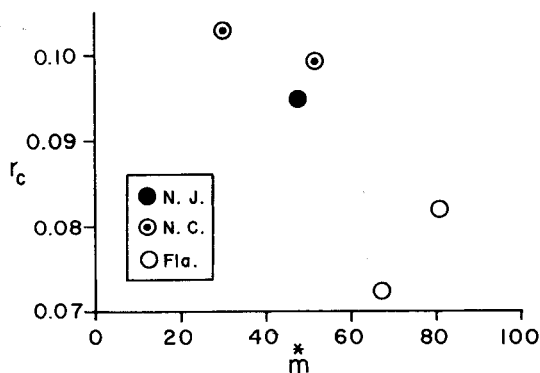


FIG. 2.—Relationship between capacity for increase (r_c) and mean crowding (\bar{m}) at the locality of origin; $r = 0.95$; $P < 0.01$.

Autogeny for the 1st (or only) ovarian cycle has been associated with the absence of suitable adult hosts (Corbet 1964, O'Meara and Edman 1975). Since *W. smithii* feed on such diverse hosts as humans and turtles, it seems unlikely that host availability is limiting for adults and the adaptive significance of hematophagy in this species probably relates to other factors.

The correlation between capacity for increase and mean crowding in Fig. 2 implies that the variation in life-history tactics of *W. smithii* between Florida and New Jersey represents an adaptive response to density. Greater crowding in the south would be emphasized by warmer temperatures which, in other mosquitoes, can result in smaller adults and lower fecundity (Clements 1963). Northern *W. smithii* live in predator-free larval habitats and, at least during the summer, develop relatively free from density-dependent constraints (Istock et al. 1976) at cool temperatures. The increase in fitness resulting from blood-feeding by large, well nourished adults would be offset by potential dangers from predation, desiccation, etc., incurred while searching for and digesting a blood meal. At more southern latitudes, the predator-free larval habitat still exists but either larval crowding, warmer temperatures, or both may result in nutritionally impoverished adults which could effect a significant increase in fitness by hematophagy. Finally, at the southern extent of their range, uncrowded leaves may not be as available as at more northern latitudes. Fitness under these conditions would not necessarily be measured by maximizing capacity for increase but rather the probability that at least some offspring would develop under less than crowded conditions. Blood feeding may enable southern *W. smithii* to increase the contribution to total reproductive effort made by the second and subsequent ovarian cycles. In that case, the adaptive significance of hematophagy in the pitcher-plant mosquito may well relate to extending the time over which individual adults could exploit potential oviposition sites.

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