

eventually destroyed the tumor cells and were shown to be cytotoxic also to various human tumor cell lines. Similarly, peripheral blood leukocytes from patients with Burkitt's lymphoma responded in vitro to autochthonous tumor cells with increased DNA synthesis and cytotoxicity, but the progenitor leukocytes did not exert cytotoxicity before in vitro stimulation (17). The parallelism between these findings and the results reported here would support the view that lymphocytes sensitive to tumor antigens may be present in both animal and human hosts and that, although these lymphocytes may be inefficient in vivo in suppressing tumor growth, they have the potential of mounting a strong cytotoxic reaction after stimulation in vitro.

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Blood-Feeding Requirements of the Mosquito: Geographical Variation in *Aedes taeniorhynchus*

Abstract. *Wild populations of Aedes taeniorhynchus were polymorphic for the diets required for ovarian development. In Aedes taeniorhynchus populations from mangrove swamps, most females possessed the capacity to produce eggs on a blood-free diet. But where the grassy salt marsh was the mosquito's principal habitat, most females lacked this capacity. Both kinds of females could utilize a blood meal for egg production.*

In biting flies such as mosquitoes (Culicidae), blackflies (Simuliidae), sand flies (Ceratopogonidae), and horseflies (Tabanidae), only the females take blood. Males do not have biting or piercing mouthparts and usually feed on plant nectars. The females also feed on plant sugars, but, with numerous exceptions, ovarian development is dependent on a blood meal. Many blackflies of the arctic and subarctic regions have only vestigial biting mouthparts and are nonfeeders as adults (1). Some of the ceratopogonids of these regions show similar modifica-

tions (2). Even when equipped for blood-feeding, some species do not need a blood meal to develop and lay an initial egg batch. This capacity, which is called autogeny, occurs in all four of the families mentioned above (1, 3, 4).

We report that *Aedes taeniorhynchus* populations from mangrove swamps have a much greater capacity to produce eggs on a blood-free diet than those populations occurring in grassy salt marshes. The North American distribution of this species ranges from the equator to 41°N latitude. The

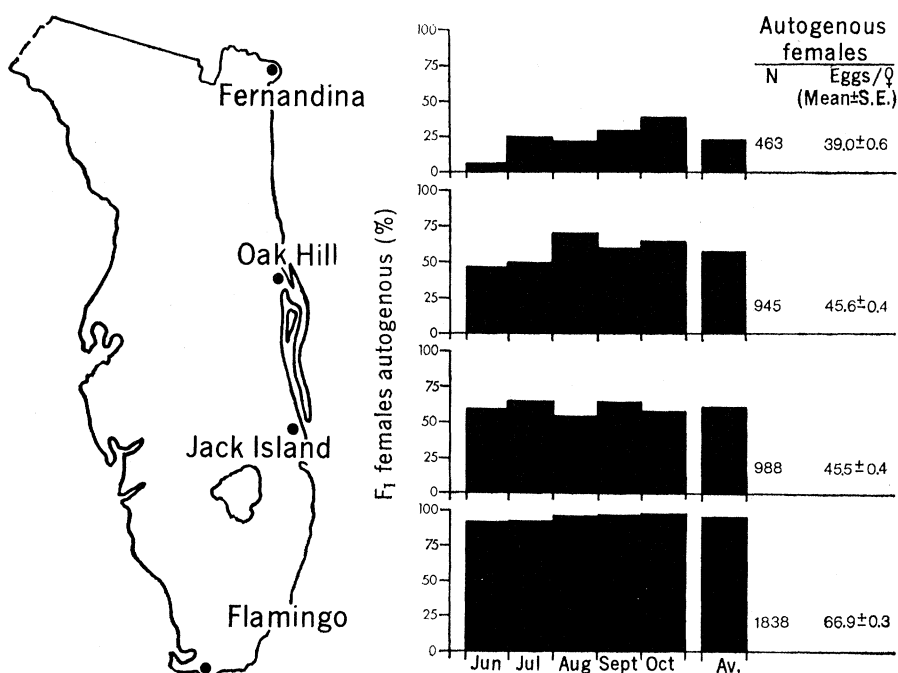


Fig. 1. The frequency and the expression of autogeny in *F₁ A. taeniorhynchus* females derived from biting collections at four coastal sites in Florida. Monthly field collections were made at each site from June through October 1971.

mangrove swamp is the principal habitat of *A. taeniorhynchus* in the tropics and subtropics, whereas the grassy salt marsh is the mosquito's major habitat in the temperate region. Thus *A. taeniorhynchus* is unlike several other North American mosquitoes in which autogeny is common in northern populations but absent or rare in southern populations (4, 5).

We examined the geographical and temporal distribution of autogeny at four sites in Florida (Fig. 1). One site (Fernandina) was a salt marsh with mosquitoes breeding in salt marsh grass (*Spartina patens*) and salt grass (*Distichlis spicata*), while another site (Flamingo) was a mangrove swamp where aquatic stages of *A. taeniorhynchus* occurred in areas dominated by black and white mangroves (*Avicennia nitida* and *Laguncularia racemosa*) and buttonwood (*Conocarpus erecta*). Two sites (Oak Hill and Jack Island) were within the region of biotic transition, and they contained mangroves, grasses, and also large areas of pickleweed (*Batis* and *Salicornia*).

We took monthly biting collections from all four sites during the principal breeding season (June through October). Single collections were made from salt marshes in Georgia (Chatham County) and New Jersey (Atlantic and Ocean counties) and from mangrove swamps in the Cayman Islands and Puerto Rico.

Each wild-caught female was blood-fed and isolated for egg-laying. Its F_1 progeny, reared under standardized conditions, was examined for the frequency and expression (fecundity) of autogenous egg development (6).

In Florida, collections from Fernandina gave F_1 progeny that had the lowest frequency of autogeny (average, 23 percent), while those of Flamingo displayed the highest frequency of autogeny (average, 95 percent). The F_1 progeny derived from Oak Hill and Jack Island were intermediate, autogeny averaging about 60 percent. Similarly, the expression of autogeny, measured by the number of eggs developed, increased along a north to south gradient (Fig. 1). The mean number of eggs developed (autogenous fecundity) of F_1 Flamingo females was nearly twice that of F_1 Fernandina females. Between November 1971 and April 1972, we revisited each field site to collect overwintering eggs. The frequency and the expression of autogeny in females obtained from these eggs

were essentially the same as those shown in Fig. 1.

Outside of Florida, we found the following frequencies of autogeny: New Jersey, 4 percent; Georgia, 8 percent; Cayman Islands, 92 percent; and Puerto Rico, 85 percent. These percentages are based on the ovarian examinations of 100 to 500 females derived from each location.

Inadequate larval and adult nutrition reduces or eliminates autogenous egg production. But since we used a single highly nutritious diet, the observed differences in frequency and expression of autogeny must be genic. From grassy salt marsh sites (New Jersey, Georgia, and Fernandina) to sites in the region of biotic transition (Oak Hill and Jack Island) to mangrove sites (Flamingo, Cayman Islands, and Puerto Rico) the females appear to have genotypes with progressively greater capacities for producing autogenous eggs.

Spielman (7) found sympatric autogenous and nonautogenous populations of the *Culex pipiens* complex to be reproductively isolated in nature.

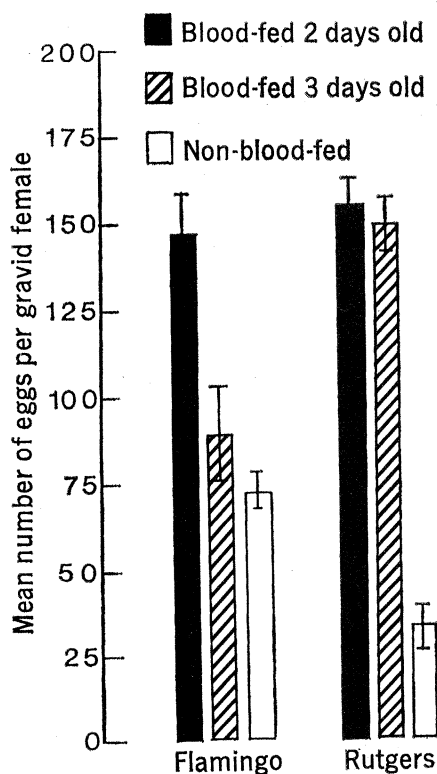


Fig. 2. Egg production in blood-fed and in non-blood-fed mosquitoes of two strains of *A. taeniorhynchus*. For each strain, 90 females (30 for each condition) were examined. Mosquitoes blood-fed on humans. Brackets indicate the 95 percent confidence interval for the mean.

Each female produced a progeny which was nearly always completely autogenous or nonautogenous. This is not the situation in *A. taeniorhynchus*. We found that 178 females from a total of 214 tested gave progeny which contained both types of females. The frequency of such mixed progeny exceeded 50 percent at each field site (Cayman Islands, Flamingo, Jack Island, Oak Hill, and Fernandina). From this type of evidence, we conclude that the two types of females can and frequently do occur in the same reproductive population.

For the production of more than one egg batch, autogenous females must take a blood meal. Figure 2 shows that even during the development of the initial egg batch, blood-feeding can significantly increase egg production. The mosquitoes used in this experiment were reared in the laboratory with the standard larval diet (6). As adults they fed ad libitum on 10 percent sugar solution. On the second and third days after emergence, approximately 35 females from each strain were selected at random and removed from the stock cages. They were placed in separate containers where they were allowed to feed on humans. The vast majority of these females readily took a blood meal. Ovarian examinations of 100 sugar-fed females from each strain gave an autogeny rate of 97 percent in Flamingo and 4 percent in Rutgers. Thus nearly all of the blood-fed Flamingo females contained genotypes for autogeny, whereas just the opposite was true of the blood-fed Rutgers females. In the Rutgers strain the mean egg production of blood-fed females was much greater than that of sugar-fed autogenous females. Flamingo females that blood-fed on the second day after emergence also showed enhanced egg production. However, when 3-day-old Flamingo females were blood-fed, there was little, if any, net gain in fecundity over that of non-blood-fed autogenous females (Fig. 2). We have examined the influence of a blood meal on the size of the initial egg batch in two other highly autogenous strains, and the results were similar to those obtained with the Flamingo strain. Apparently for autogenous *A. taeniorhynchus* the degree of flexibility in oogenesis diminishes with age.

Most theories that attempt to account for the occurrence of autogenous mosquitoes emphasize environmental factors that prevent blood-feeding.

Either the absence of suitable hosts or the inhibition of host-seeking by harsh climatic conditions would make autogeny the only means for population survival. In the variable and at times severe climatic regions of the temperate and arctic zones, both of these factors definitely appear to be major forces selecting for autogeny (8, 9).

The present report is the first to describe a distribution where the capacity to produce autogenous eggs increases from northern to southern populations. Little is known concerning the relative influence of specific environmental factors on the occurrence of autogeny in field populations of *A. taeniorhynchus*. Yet preliminary evidence indicates that even in this species host scarcity might be an important factor selecting for autogeny. For example, Edman (10) recently found that in east-central Florida *A. taeniorhynchus* feeds primarily on mammals. More than 80 percent of the identified blood meals were from rabbits and ruminants. Neither type of mammalian host was abundant in the immediate coastal areas of this region, and blood engorgement rates were very low, but 8 miles (13 km) inland suitable hosts were more numerous and blood engorgement rates were three times higher (10). There is a definite need for additional studies on mosquito-host interrelations. Such studies would certainly improve our understanding of

the influence of host abundance on the frequency and expression of autogeny in *A. taeniorhynchus*.

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6. Aquatic stages were reared in enamel pans which contained 350 ml of water and 80 larvae. Synchronous larval development in 6 days was achieved with the use of a diet composed of 1 part powdered brewers' yeast, 1 part lactalbumin, and 1 part pulverized Lab Chow. This mixture was put in each pan according to the following schedule: day 1, 1 unit; day 2, 1 unit; day 3, 3 units; day 4, 4 units; day 5, 4 units (1 unit equals 50 mg). Upon emergence, females were isolated in glass vials and allowed to feed ad libitum on 10 percent sugar solution. Ovarian examinations were performed on females which were at least 5 days old. Only development to stage V was classified as autogenous. For a description of mosquito ovarian stages, see S. R. Christophers [*Paludism* **2**, 73 (1911)].
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Dynamics of Number Fluctuations: Motile Microorganisms

Abstract. *The time dependence of the intensity of light scattered from motile Escherichia coli bacteria is studied in population densities so low that the intensity autocorrelation function reflects fluctuations in the total number of particles in the scattering region. Measured correlation functions are analyzed by using a random walk model of bacterial motion.*

It has recently become apparent that important information on the dynamic properties of microscopic particles can be obtained by study of the time dependence of the fluctuating intensity of light scattered from systems in which the total number of particles varies with time (1). When $\langle N \rangle$, the average number of particles in the illuminated scattering region, is of order unity, a very slowly decaying mode appears in the intensity correlation function, due to fluctuations in the total number of scatterers in the scattering volume (occupation number fluctuations). The characteristic time of this mode re-

flects the residence time of a typical particle in the scattering region. In this report, experimental data are presented on the dynamics of occupation number fluctuations for motile (swimming) microorganisms. These data are interpreted by using a random walk model of particle motion.

The work reported here represents a useful biological application of a very general method. Although the most promising application of this method is in the area of chemotaxis and phototaxis, fluctuations due to chemical reactions (2) and turbulence can be studied by analogous techniques. In fact, these

methods apply whenever the number of particles under study is small (say less than 20), or their relative positions are correlated over distances of the order of 1 μm , or both.

Although modern photon counting techniques are employed here, the experiments could in principle have been performed by a patient observer equipped with only a microscope. The observer would record (at half-second intervals) the number of bacteria appearing in a well-defined volume. In the work reported here, the measurement of scattered light intensity merely provides a convenient way to "count" particles.

The total field scattered at time t by a system of M identical, isotropic particles is proportional to a properly weighted sum of the phase factors introduced by each particle,

$$E(K, t) = \sum_{j=1}^M \mathcal{E}(\mathbf{r}_j) \exp [i\mathbf{K} \cdot \mathbf{r}_j(t)] \quad (1)$$

where $\mathbf{r}_j$ is the position of particle j , $\mathcal{E}(\mathbf{r})$ is the amplitude of the field scattered by a particle when at position $\mathbf{r}$, i is the imaginary unit, and $\mathbf{K}$ is the scattering vector. For incident light of wave vector $\mathbf{K}_0$, $K = 2K_0 \sin (\theta/2)$, θ being the scattering angle and K and K_0 the magnitudes of the vectors $\mathbf{K}$ and $\mathbf{K}_0$. In the experiments reported here, the scattering region is defined in two dimensions (x, y) by a focused laser beam and in the third dimension (z) by a narrow collection slit. For this configuration, $\mathcal{E}(\mathbf{r})$ can be represented by

$$\mathcal{E}(\mathbf{r}) \propto \exp \{ -(x^2 + y^2)/\sigma_1^2 - z^2/\sigma_2^2 \} \quad (2)$$

where σ_1 and σ_2 are the points where the intensity profile of the incident beam and the transmission profile of the slit are $1/e^2$ of their initial values. Diffraction at the slit produces the approximate Gaussian profile in the z direction.

Since the scattered intensity $I(t)$ is proportional to $|E(t)|^2$, the correlation function $\langle I(0)I(t) \rangle$ of the scattered intensity follows directly from Eq. 1. If $K^{-1} \ll (\sigma_1, \sigma_2)$,

$$\langle I(0)I(t) \rangle \propto \langle N \rangle^2 + \langle N \rangle^2 |F(K, t)|^2 + \langle \delta N(0) \delta N(t) \rangle \quad (3a)$$

$$\langle \delta N(0) \delta N(t) \rangle = \rho \int \int d\mathbf{r}_1 d\mathbf{r}_2 \mathcal{E}^2(\mathbf{r}_1) \mathcal{E}^2(\mathbf{r}_2) p(\mathbf{r}_2 - \mathbf{r}_1; t) \quad (3b)$$

where ρ is the number density of scatterers and $\langle N \rangle = \pi^{3/2} \sigma_1^2 \sigma_2 \rho$ is the average number of particles in the scat-