Autogeny in Panamanian *Phlebotomus* Sandflies (Diptera: Psychodidae)[1]

PHYLLIS T. JOHNSON

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Autogeny in Panamanian *Phlebotomus* Sandflies (Diptera: Psychodidae)[1]

PHYLLIS T. JOHNSON

Gorgas Memorial Laboratory, Panamá, República de Panamá

ABSTRACT

In the course of leishmaniasis studies at Gorgas Memorial Laboratory females of *Phlebotomus gomezi* Nitz., one of the laboratory-reared species, occasionally were discovered producing fertile eggs without a previous blood meal. Nine autogenous strains of this species, one reaching the 11th generation, have been maintained in laboratory culture. Autogenous females do not need any form of food as adults and apparently produce eggs by utilizing the well-developed fat body, which never shows comparable development in normal, anautogenous females. Normal strains of *P. gomezi*, some now in the 13th laboratory generation, have never been observed to reproduce autogenously in the laboratory. Attempts at reciprocal crossing indicate that autogenous and normal individuals of the laboratory strains do not interbreed, or at least do not produce fertile eggs. Autogenous females are found in nature in small numbers throughout the year.

The production of viable eggs without a previous blood meal by a bloodsucking insect was first noted in the mosquito *Culex pipiens* by Roubaud and Toumanoff (1930), a phenomenon for which they proposed the term *autogeny*. To date autogeny has been reported to occur in several dipteran species representing various members of the Culicidae and the genera *Culicoides*, *Simulium*, and in *Phlebotomus papatasi* Scop. from Russia. It is quite possible that autogeny occurs in many more bloodsucking dipteran species but it would be difficult if not impossible to demonstrate its occurrence in a wild population, and even during the process of laboratory rearing it might be overlooked unless a special search were undertaken.

The present paper constitutes a report of autogeny in a Panamanian species of *Phlebotomus*. In connection with leishmaniasis studies at Gorgas Memorial Laboratory, several species of Panamanian *Phlebotomus* sandflies have been established and maintained in successive laboratory cultures. One of these species, *P. gomezi* Nitz., occasionally lays fertile eggs without a previous blood meal. We have maintained nine autogenous strains of this species, the oldest having passed through 11 laboratory generations. Each strain was from a different female or pool of two to five females, at least one of which was autogenous.

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MATERIALS AND METHODS

The autogenous and anautogenous, or normal, strains of *gomezi* in our laboratory were all derived from wild-caught females which had recently fed on man or horse, or were gravid when collected from resting places in the jungle. Wild-caught females were maintained separately in large, moistened, plaster-lined vials, in which they oviposited. Eggs from those females identified as *gomezi* were left for rearing in the original vials, or two or more batches of eggs were transferred to our standard breeding vessel, a plaster-lined earthenware pot.

Larval food consisted of autoclaved, dried and ground rabbit feces which had been soaked in human blood, or of an autoclaved mixture of ground rabbit feces, decaying forest leaves and dried insects.

Adults of the first laboratory generation (progeny of the wild-caught females) and succeeding laboratory generations were allowed access to a boiled raisin; females of the normal strain were allowed a blood meal.

CHARACTERISTICS OF THE AUTOGENOUS STRAIN

Males and females of the autogenous and normal strains have been compared by Dr. G. B. Fairchild, of our staff. He has been unable to find any morphological differences between the two strains.

In comparing the length of life cycle of autogenous and normal strains the only difference seems to be a lengthening of the egg stage. Of 81 normal females, 66 laid eggs which hatched in 6 to 8 days; 15 produced eggs which hatched in 9 to 10 days, while eggs from two females did not hatch until 11 and 12 days, respectively. Of five autogenous females, two laid eggs which hatched in 8 days, one in 10 days, one in 11 days, and one only after 14 days.

Autogenous females will suck blood both in nature and in the laboratory. Of the nine autogenous strains we have had in the laboratory at various times, all but one came from eggs produced by females known to have had a blood meal. That blood was not necessary for egg production seems indicated by the fact that four of the nine females laid eggs only 3 days after the blood meal. It is probable that egg development was already under way at the time of feeding, since normal *gomezi* rarely produce eggs in less than 4 days and usually take 5 to 8 days under laboratory conditions.

On the average, autogenous females produce fewer eggs than do normal ones. Most normal females lay from about 15 to 40 eggs, with extreme ranges of from 1 to 70 (based on 208 observations). Fourteen autogenous females laid from 4 to 22 eggs.

The dissection of 40 autogenous females and over 200 normal females, ranging in age from newly emerged to 72 hours, has revealed one constant difference between the two groups. The autogenous females invariably have a well-developed fat body at the time of emergence. Normal *gomezi* females never have a fat body which is discernible with the dissecting microscope. Dolmatova (1946), who was the first to observe autogeny in a species of *Phlebotomus*, did not mention the relative development of the fat body in her series of autogenous and normal females. She did observe that of eight laboratory-reared, unfed *papatasi* females, from eastern Georgia, two laid viable eggs autogenously and furthermore, 18 of 21 laboratory-reared, unfed females underwent development to varying degrees of the ovaries.

Females of the autogenous strains need no source of food as adults in order to lay viable eggs. The larval food given in the laboratory is a mixture rich in nitrogenous material, particularly in the case of the food with added blood. However, it appears that autogenous development in *gomezi* is not a response to the concentrated food. Our normal strains, some of which are now in the 13th laboratory generation, have been maintained on the same diet as the autogenous strains and have never been observed to reproduce autogenously.

THE FREQUENCY OF AUTOGENY IN WILD POPULATIONS

Some of our autogenous strains came from an experimental series undertaken with the express purpose of obtaining some indication of the incidence of autogeny in *gomezi* taken in our routine field collections. A large number of such wild-caught females were kept separately from the time they arrived in the laboratory. Over a period of nearly a year, 11 June 1959 to 8 May 1960, a total of 113 wild-caught *gomezi* females, all of which had taken a blood meal from man or horse in the field, laid eggs in their individual plaster-lined vials. The eggs hatched and the larvae, with blood-soaked rabbit feces as food, were reared to the adult stage. These adults were kept in their original vials, without access to any blood meal, until all had died. The vials were then examined for the presence of eggs or young larvae. The absence of either eggs or larvae was taken as an index of a normal strain.

Of the 113 females, 5 (4.4 percent) produced autogenous offspring. The dates of collection of these five were 16 June, 24 November, 1959, 8 February, 7 and 14 March, 1960. For the calendar months in which autogenous females were found, there were 1 autogenous of 2 females collected in June, 1 of 2 in November, 1 of 50 in February, and 2 of 46 in March. The rest of the 113 females were scattered throughout other months. Two areas in the Canal Zone and one in the Republic of Panama were represented. While our samples are small, there is no obvious correlation between the time of year or locality of collection and the proportion of autogenous to normal females.

ATTEMPTS TO CROSS AUTOGENOUS AND NORMAL STRAINS

Various workers have found that strains of autogenous and anautogenous *Culex pipiens* are interfertile (Weyer 1936, Rozeboom and Gilford 1954). In order to ascertain whether the same is true of our *P. gomezi* strains the following tests were made.

Pupae of an autogenous and a normal strain, both of the seventh laboratory generation, were maintained individually until adult emergence to assure a supply of virgin males and females. Upon emergence a male of one strain and female of the other were placed together in a rearing vial. Crosses of 9 autogenous ♂♂ x 9 anautogenous ♀♀ and of 14 anautogenous ♂♂ x 14 autogenous females were made. The females of the normal strain were allowed a blood meal, and all members of the series had access to a boiled raisin. Eggs were laid by all the females, both autogenous and normal. None of the eggs hatched. Controls consisted of a paired male and female of each of the two strains. They were maintained under conditions similar to the test series except that the autogenous pair did not have access to a raisin. Both control females laid eggs which hatched into healthy larvae.

To test whether the lack of interstrain fertility might be caused by the reluctance of mixed strains to mate in a small container, a second series was carried out, utilizing rearing pots rather than vials. Ninth generation males and females from isolated pupae and of the same autogenous strain as above, but of a different normal strain, were placed together in reciprocal crosses in two rearing pots. Seven autogenous ♂♂ x three fed anautogenous ♀♀ produced 58 eggs, none of which hatched. Eight anautogenous ♂♂ x thirteen autogenous ♀♀ produced 135 eggs, none of which hatched.

It has not been determined whether the cause of interstrain sterility is lack of mating or physiological incompatibility. Two methods of demonstrating mating would be either to observe pairs in copula or to find sperm in the spermathecae. I have never observed *P. gomezi*—either autogenous or normal—in copula in the laboratory. *Gomezi* females of both the normal and autogenous strains which had laid fertile eggs, and hence had mated, nevertheless rarely contained sperm in the spermathecae when dissected. Of 3 autogenous and 19 normal females of varying ages, with males continuously present, none of the autogenous and only two of the normal females had sperm in the spermathecae.

DISCUSSION

The role of autogeny in the population dynamics of insects which are ordinarily obligate bloodsuckers has not been ascertained. Autogeny might aid insects, such as sandflies, to maintain their populations during periods of stress, as, for example, a sudden reduction in numbers of hosts, or periods of unfavorable weather when the insect might be less able to leave its shelter to seek a blood meal, as in prolonged stormy weather or severe drouth.

Since the samples of *P. gomezi* in this study were not homogeneous and do not lend themselves to statistical analysis, it can only be said that a small percentage of females reproduce autogenously both during the rainy season, May-December, and the dry season, January-April.

At the present time we do not know whether autogeny in *gomezi*, which is apparently a genetically controlled phenomenon, is a multiple factor or blending type of inheritance, as may be the case in *C. pipiens* (Spielman 1957). The presumptive laboratory evidence for lack of interbreeding between established autogenous and anautogenous strains points to the possibility that the genetic basis for autogeny in *gomezi* may be different from that found in *C. pipiens*. Further experiments involving wild-caught females with a heterogeneous gene make-up will be necessary before more can be said regarding the genetics of *P. gomezi* autogeny.

It is not known whether the phenomenon of autogeny occurs throughout the entire range of *gomezi*, which is from Nicaragua to the Amazon. Dolmatova (1946), working with *Phlebotomus papatasi* from two areas in Tadzhikistan and one area in eastern Georgia, observed autogeny in the Georgian population but none in populations from the two areas in Central Asia.

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