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## THE PATTERN OF A HOST-PARASITE DISTRIBUTION

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**ABSTRACT:** The pattern of density of the microfilaria *Chandlerella quiscali* among host specimens of the gnat *Culicoides crepuscularis* was fitted to the negative binomial distribution. Variations in the density of microfilariae in peripheral circulation of the grackle *Quiscalus quiscula versicolor* were suggested as the reason for the clumped density of nematodes among the gnats.

Analyses of variations in pattern of distribution have been applied to plant and animal populations to gain insight to some of the biological interactions that vary over time and space: (e.g., Kershaw, 1964; Greig-Smith, 1964; Pielou, 1969; and Crofton, 1971a, b). Three general categories of pattern may be defined as (1) regular, (2) random and (3) clumped. Each category can be tested for fit by observed sets of distribution data, and each infers certain kinds of ecological phenomena. Deviations from the random (Poisson) pattern imply an interdependent relationship among individuals or between organisms and some environmental (habitat) variable. For example, regular patterns may be seen in species that saturate habitats to the level where minimum, equal distances separate all individuals. A clumped or contagious distribution pattern can be seen where habitats are not uniform and individuals are concentrated in the most suitable patches, or where interactions among individuals may hold organisms together in groups although the habitat is uniform. Analyses of parasite populations for variations in pattern of distribution among and within host specimens provide a means of defining certain categories of parasite-parasite or parasite-host interaction, and of extending our ability to describe symbiotic relationships in general. This report describes the analysis of pattern of distribution of microfilariae (*Chandlerella quiscali*) among host specimens of the gnat (*Culicoides crepuscularis*).

### MATERIALS AND METHODS

The data for this analysis came from the study by Robinson (1971) on the role of the ceratopogonid gnat *Culicoides crepuscularis* as a host for the filarial nematode *Chandlerella quiscali* that

parasitizes the purple grackle, *Quiscalus quiscula versicolor*. In that study, 2 kinds of traps and a variety of trapping times were used to expose and collect the *Culicoides*. However, the data for the present paper include only 143 gnats from the total collection, that were taken under a single set of standard conditions.

The same infected bird was used for all exposures. The microfilarial density in its peripheral blood during the hours of trapping was not determined, but relative to infections studied in many other birds this one was light to moderate. The trapping time was 2100 to 2300 hr, a period of the day in which it was known that gnats were maximally active, and in which the nocturnally periodic microfilariae were swarming in the peripheral blood of the host. Traps were run on nights in June and July.

A modified funnel trap was used, in which 12 birds were contained as attractants, but the gnats could only reach the infected bird to feed. Three of these traps were run in different ecological situations and heights, known from previous work to be well populated by the gnats. Exposed gnats were separated from the unengorged ones, and maintained on honey water in small cages until killed for dissection and examination. There was no detectible mortality among the gnats during the developmental period of the worms, and likewise no mortality among the nematodes. Unengorged gnats served as controls and none contained microfilariae. The large number of gnats,  $n = 143$ , provided a sample size sufficient for statistical treatment.

The raw data were tabulated in three ways. First all of the 143 gnats sampled were treated as a set for calculation of a sample mean and variance. Second, only those 85 gnats containing nematodes were tested for fit to a truncated (the zero frequency class was not included) Poisson distribution. Finally, all 143 gnats were separated into frequency classes by the numbers of contained nematodes and statistical testing was done for fits to the Poisson and the negative binomial (clumped) distributions.

### RESULTS

The mean number,  $\bar{x}$ , of nematodes per gnat was equal to 2.61, and the variance,  $s^2$ ,

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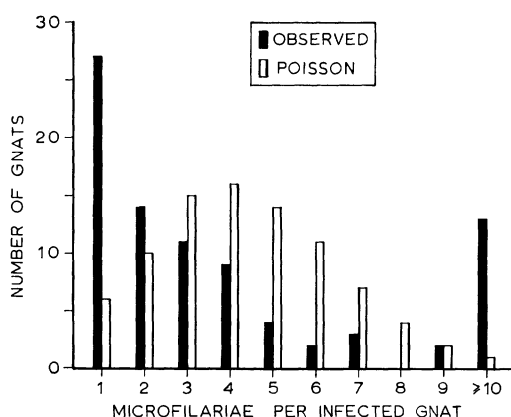


FIGURE 1. Observed and Poisson-expected frequencies of microfilariae among infected gnats.

was 17.43. The ratio of  $s^2/\bar{x}$  is expected to be unity if the sample represents a random distribution because the expected variance of the Poisson distribution is equal to its mean. It is therefore easy to test the observed fre-

quencies for fit because  $s^2/\bar{x}$  is distributed as a test statistic according to probabilities of chi-square over degrees of freedom. For the 143 gnats scored,  $s^2/\bar{x}$  was equal to 6.68, and was significantly different from the expected chi-square at a probability level less than .001. This meant that the overall pattern of observed frequencies did not fit the Poisson probability distribution.

A second test was performed on a subset of these data whereby only infected gnats were included. This was done to see whether randomness existed among infected gnats as might be the case if, for example, a portion of the gnat population were immune to infection by the nematodes. The average number of microfilariae per infected gnat was 4.4 and was used to test for fit to the Poisson frequencies from the tables of Molina (1942) rather than using the method of Plackett (1953). The goodness-of-fit test was done according to Cochran (1954) in order to strengthen the chi-square statistic. The ob-

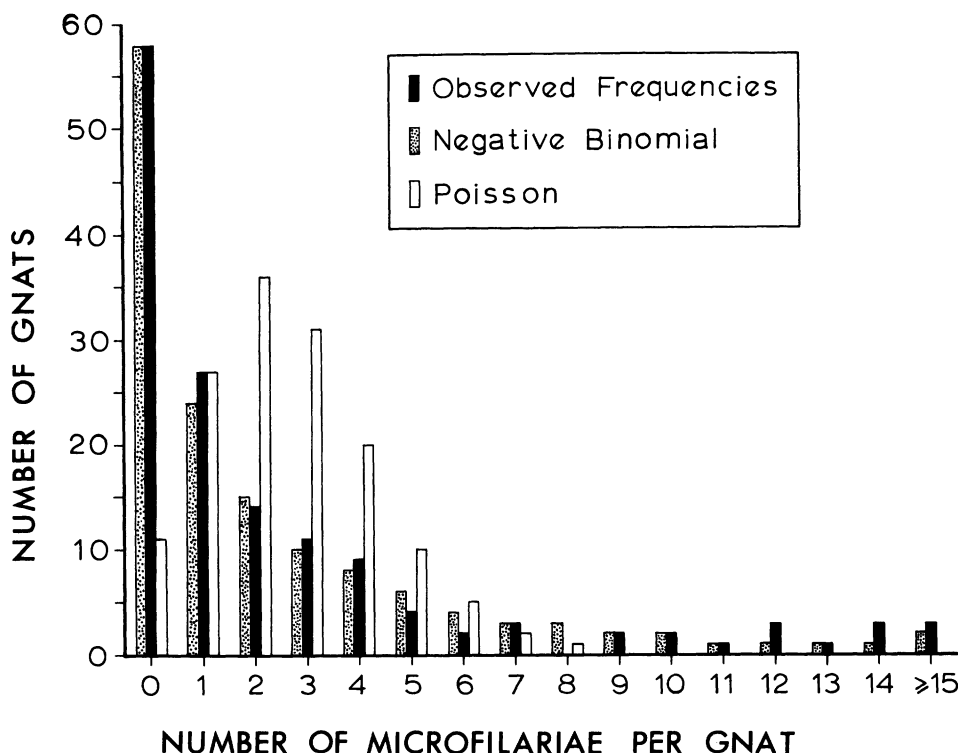


FIGURE 2. Observed, Poisson-expected and negative binomial-expected frequencies of microfilariae among gnats.

served and Poisson-expected frequencies of Figure 1 showed poor correspondence that was reflected by the very high chi-square value of 245.1. This meant that neither the overall pattern nor the truncated pattern of nematodes per gnat could be adequately fitted to a random distribution.

Some type of clumped distribution was indicated as a logical alternative to the random distribution by the high variance:mean ratio. The negative binomial distribution has been used as an alternate when clumping appears because of its relative ease of fit; (e.g., Fisher, 1941; Skellam, 1952; Bliss, 1953; Lloyd, 1967; Siniff and Jessen, 1969; Uzzell and Corbin, 1971; and Crofton, 1971a, b). The distribution is defined by two parameters, the arithmetic mean ( $\mu$ ) and a positive exponent ( $k$ ). The observed sample mean ( $\bar{x} = 2.61$ ) was used to estimate  $\mu$ , and  $k$  was estimated to be 0.4885 by the ratio of uninfected:infected gnats according to the procedure of Bliss (1953). The result of this fit is seen in Figure 2, where the observed frequencies are plotted along with expected values for both the Poisson and the negative binomial distributions. The chi-square test statistic for goodness-of-fit to the negative binomial was not significantly different from expected.

### DISCUSSION

The negative binomial can be obtained as either a generalized or a compounded distribution, and as discussed by Pielou (1969), cannot be used to define mechanisms responsible for the generation of observed frequency patterns solely because of its good fit to empirical data. However, the fit of the pattern of observed frequencies of nematodes per engorged gnat to a clumped pattern has certainly ruled out patterns that are strictly random or regular.

The clumped nature of these data may be explained in at least four ways. First, the microfilariae may have been circulating at a constant density, but were aggregated into groups within the blood vessels where the gnats fed. Second, the microfilariae may have been random in their pattern, but their density may have varied at different sites in the peripheral circulation. Third, the nematodes were randomly distributed and of constant density

over both time and sites of feeding, but some of the gnats may have injected an attractant substance that promoted higher rates of infection. And fourth, the nematodes may have been random throughout the peripheral circulation, but their density may have varied during the 2-hr periods of exposure to the gnats. This last model seems to be the most appropriate.

Odetoyinbo (1960) and Odetoyinbo and Ulmer (1960) have found that this species of microfilaria is highly nocturnal in its appearance in the peripheral circulation of the grackle. But more important, the density of this nematode was shown to vary a great deal for the same sampling time on successive nights. For example, a 0.0125 ml sample of blood from a grackle contained only three microfilariae at 2200 hr on one night and 208 at the same time on the next night. In general, Odetoyinbo demonstrated that even though the same birds were sampled at the same time on successive nights, the observed variations in microfilariae were great enough to question the assumption of constant density. Such variation in nematode density could account for the observed clumped pattern of their frequency among gnats that were collected by Robinson (1971) after exposure to his grackle between 2100 and 2300 hr. Pacheco, Atkins, and Gurian (1972) demonstrated good correspondence between numbers of microfilariae ingested by ticks and the quantity of their blood meal; i.e., microfilariae were neither attracted nor repelled by the salivary secretions. This report is quite consistent with the results of our analysis that has shown a fit to the negative binomial, and added support to our suggestion that temporal variations in density are responsible for the clumped pattern of microfilariae among the gnats. The evolutionary significance of a clumped pattern of parasites among host organisms has been recently proposed.

Crofton (1971a) was able to fit the infective pattern of the acanthocephalan, *Polymorphus minutus*, in amphipods, *Gammarus pulex*, to a truncated negative binomial distribution. He truncated his distributions at high, variable levels of infection to account for parasite-induced mortality. Crofton felt that the importance of this clumped pattern of dispersion

allowed for the maintenance of an equilibrium between populations of parasite and host whereby the parasite was a regulator of the host population. He proposed that an overdispersed (clumped) pattern of parasites among hosts was of such fundamental importance that it should be incorporated into the definition of parasitism. Crofton (1971b) tested the importance of the characteristic pattern by modeling parasite and host population densities, and found that the greatest control by the parasite species was realized when ( $3 > k > 1$ ), where  $k$  is one of the parameters of the negative binomial distribution. Our data are consistent with Crofton's views, despite the fact that we were working with low levels of infection. The general acceptance of his model will depend upon the collection and analyses of basic ecological data from host-parasite populations. Regardless of this however, Crofton has supplied us with a powerful set of testable hypotheses and has demonstrated the importance of pattern analysis in the study of parasitism.

#### ACKNOWLEDGMENTS

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