THE DISTRIBUTION OF THE EGGS OF THE SORGHUM SHOOTFLY, *ATHERIGONA SOCCATA* RONDANI (DIPTERA:MUSCIDAE)

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Abstract—Field and laboratory observations revealed that the placement of eggs of the sorghum shootfly, *Atherigona soccata*, among sorghum stems tended to be random or slightly aggregated rather than regular, which suggests that the site of oviposition by a female is little or not determined by the presence of other eggs already laid. The possible effects of this type of distribution on the mortality of the first-instar larvae are briefly discussed.

Key Words: Sorghum shootfly, oviposition, distribution of eggs, *Atherigona soccata, Sorghum bicolor*

INTRODUCTION

THE DISTRIBUTION of eggs of the sorghum shootfly, *Atherigona soccata*, has an important bearing on the larval survival and on the subsequent distribution of damage among sorghum plants because only one first-instar larva can develop in a single stem. As in many Diptera, *A. soccata* females lay their eggs singly on sorghum leaves and usually fly off after each oviposition; in a number of Dipteran species, specially in fruit-infesting Tephritids, it has been observed that a regulating mechanism exists, which prevents overcrowding of larvae in the available host fruits. The females tend to avoid fruits where an egg has already been placed, so that the egg distribution is not excessive for the food available to the larvae (MARTIN 1948; HAEFLINGER 1953). This regulating mechanism has been shown to be an oviposition-deterring pheromone deposited by the female on the egg or around it during oviposition or immediately after (PROKOPY, 1972, 1975; KATSOYANNOS, 1975). It should be noted, however, that in a great number of other insects, including some belonging to the same Tephritid family (PRITCHARD, 1969), it has been demonstrated that the actual distribution of eggs was not uniform but rather random or even aggregated (BARDNER and LOFTY, 1971; ARBOGAST and MULLEN, 1978; PIETERS and STERLING, 1974).

Preliminary studies of natural populations of the sorghum shootfly at the ICIPE Mbita Point Field Station (Nyanza Province, Kenya) have shown that shoots bearing several eggs (up to nine) are common in the field. However, recent work (RAINA, 1981) shows that an oviposition deterrent also exists in *A. soccata*; it was therefore decided to investigate the distribution pattern of eggs of the sorghum shootfly, both under natural conditions and in the laboratory.

MATERIALS AND METHODS

In laboratory experiments, groups of 64 seedlings of a susceptible variety (CSH-1) of the same age, grown in glass vials (2.5 × 7.5 cm) were presented to four gravid females from a colony fed with glucose and brewer's yeast and periodically provided with plants for oviposition; the duration of exposure was varied to provide different egg densities. The number of eggs laid on each plant was recorded on each occasion and plants were discarded after each test. The temperature in the cages ranged from 25 to 31°C and the air humidity from 65 to 75%. Egg distribution was also recorded under natural conditions: unhatched eggs were counted on young seedlings in small plots located at Nairobi and at Mbita Point between November 1978 and June 1979. Counts were made before the first dead-hearts appeared, so that their possible attractant or repellent influence might be avoided and also to ensure that the number of eggs already hatched was low and had a negligible effect on the observed distributions. Each plot contained similar numbers of plants (between 60 and 100) to allow the comparison of the different values of *k* (HARCOURT, 1961).

The observed distributions were compared to the Poisson and Negative Binomial distributions; the Poisson distribution occurs when one organism has equal chances of being in each of several units, when the presence in a unit of one individual does not influence the distribution of the others; it is found in many insect populations (WADLEY, 1950; SOUTHWOOD, 1966). The Negative Binomial distribution is met in numerous biological situations where a certain amount of clumping or aggregation of the organisms occur in an otherwise randomly distributed population (KEMPTHORNE, 1973).

The comparison between the observed distributions and the corresponding Poisson distribution was made by a chi-square equation:

$$\chi^2 = n\,\frac{s^2}{\bar{x}},$$

where n is the degree of freedom and $s^2/\bar{x}$ is the dispersion index.

The methods used to test the goodness of fit of the Negative Binomial distribution to the observed data are those given by BLISS and FISHER (1953), which

Table 1. Effect of different densities on distribution of eggs of *A. soccata* from field-collected samples

Mean density	Variance	Discrepancy from Poisson	Discrepancy from Negative Binomial	k	$I\delta$
0.040	0.033	N.S.	—	(1)	0
0.081	0.111	N.S.	N.S.	0.160	6.167
0.088	0.107	N.S.	N.S.	0.398	3.762
0.107	0.096	N.S.	—	(1)	0
0.131	0.131	N.S.	—	(1)	1.016
0.160	0.176	N.S.	N.S.	1.483	1.667
0.210	0.208	N.S.	—	(1)	0.952
0.270	0.259	N.S.	—	(1)	0.854
0.295	0.279	N.S.	—	(1)	0.812
0.340	0.347	N.S.	N.S.	16.514	1.096
0.350	0.330	N.S.	—	(1)	0.840
0.353	0.426	N.S.	N.S.	1.562	1.587
0.400	0.424	N.S.	N.S.	8.977	1.154
0.400	0.464	N.S.	N.S.	2.086	1.410
0.412	0.650	N.S.	N.S.	0.677	2.424
0.425	0.479	N.S.	N.S.	3.145	1.306
0.450	0.411	N.S.	—	(1)	0.808
0.460	0.452	N.S.	—	(1)	0.966
0.600	0.606	N.S.	N.S.	60.000	1.017
0.645	0.757	N.S.	N.S.	3.684	1.271
0.672	0.767	N.S.	N.S.	4.582	1.212

N.S.: Not significant at the 5% level.
(1): Not calculated $s^2 \geqslant \bar{x}$.

involve the calculation of the statistics U and T, and their comparison with their own standard errors. Parameter k of the Negative Binomial distribution was estimated by the maximum-likelihood method described by ANSCOMBE (1949); its values can range from zero, where clumping is extreme, to infinity, which defines a purely random distribution of counts (WATERS, 1959); values between two and eight indicate a moderate degree of aggregation (SOUTHWOOD, 1966). Parameter 'b' of Taylor's power law (TAYLOR 1961), which is the slope of the regression line of log s^2 on log $\bar{x}$, was also calculated from field and cage data; values of b less than one indicate a regular distribution, values of b higher than two occur when there is aggregation; values of b between one and two indicate a random distribution (LAMOTTE, 1957). Morisita's index of dispersion ($I\delta$) was also calculated; in a random distribution, $I\delta$ is equal to unity; it is less than one in regular distributions and more than one in aggregated distributions (MORISITA, 1962, 1964).

RESULTS

The egg densities observed in the insectary ranged from 0.062 to 2.046 eggs per plant; the means and variances of the different samples are given in Table 2. The same table also shows that, apart from very few exceptions, all samples with a mean less than one agree with the Poisson distribution while almost all samples with higher means differ significantly from it. In these samples, the discrepancy from the Poisson distribution always arises from an excess of plants without any eggs and of plants with more than one. In the field, the observed densities were much lower and ranged from 0.040 to 0.672 eggs per plant; the

means and variances of the 21 samples are given in Table 1. None of the samples disagree with the Poisson distribution; about half of them also agreed with the Negative Binomial distribution, the others having generally a variance smaller than the mean, which does not allow the calculation of the parameter k and of the different terms of the theoretical distribution, but guarantees the randomness of the distribution.

The various calculated dispersion indexes all show the same trend: the Poisson dispersion index varies in the field between 0.89 and 1.57, suggesting a random distribution of eggs; in cage experiments, results are very similar at lower densities but show a sensible increase at higher densities (mean higher than one), the maximum being 2.72 for a mean of 2.046; this suggests an increasing degree of clumping. Parameter k exhibits much wider variations, especially in the field samples, where it ranges from 0.16 to 60; in the insectary, the variation is only from 0.09 to 3.11. If we ignore a few low values ($k = 0.09, 0.16, 0.22, 0.39$ and 0.55), which occur at very low densities and have little significance, k is always near unity or higher than unity. Higher values of k are found in the field, at densities higher than 30 eggs per 100 plants, which indicates that a higher amount of clustering occurred in cage experiments than in the field. Although it has been observed by several authors (HARCOURT 1960; WATERS, 1959; ARBOGAST, 1978) that insect populations tend to be more randomly distributed when their density increases, we did not find any correlation between k and the egg density ($r = 0.042$ for all data) in the range of densities we have observed.

Similar conclusions may be drawn from the observation of Morisita's index: apart from low-density samples, $I\delta$ consistently lies between 0.8 and 2.6 (slight aggregation); there is no noticeable difference

Table 2. Effect of different densities on distribution of eggs of *A. soccata*
from cage samples

Mean density	Variance	Discrepancy from Poisson	Discrepancy from Negative Binomial	k	$I\delta$
0.062	0.091	N.S.	N.S.	0.097	10.667
0.125	0.174	N.S.	N.S.	0.226	4.571
0.203	0.250	N.S.	N.S.	0.550	-2.461
0.312	0.376	N.S.	N.S.	1.662	1.684
0.375	0.523	N.S.	N.S.	0.856	2.686
0.390	0.495	N.S.	—	1.565	1.706
0.515	0.507	N.S.	N.S.	(1)	0.969
0.609	1.067	S*	N.S.	0.870	2.245
0.687	0.885	N.S.	N.S.	2.665	1.420
0.980	0.765	N.S.	—	(1)	0.842
0.906	1.165	N.S.	N.S.	3.042	1.316
0.937	0.853	N.S.	—	(1)	0.903
1.000	1.460	S*	N.S.	2.331	1.460
1.046	1.791	S*	N.S.	1.169	1.678
1.062	1.964	S***	N.S.	1.417	1.798
1.093	1.864	S**	N.S.	1.317	1.643
1.125	1.412	N.S.	N.S.	3.118	1.226
1.375	2.492	S*	N.S.	1.750	1.588
1.468	3.808	S**	N.S.	0.938	2.225
1.656	3.149	S***	N.S.	1.940	1.514
2.046	5.569	S***	N.S.	0.944	1.833

N.S.: Not significant at the 0.05% level.
S*: Significant at the 0.05% level
S**: Significant at the 0.01% level.
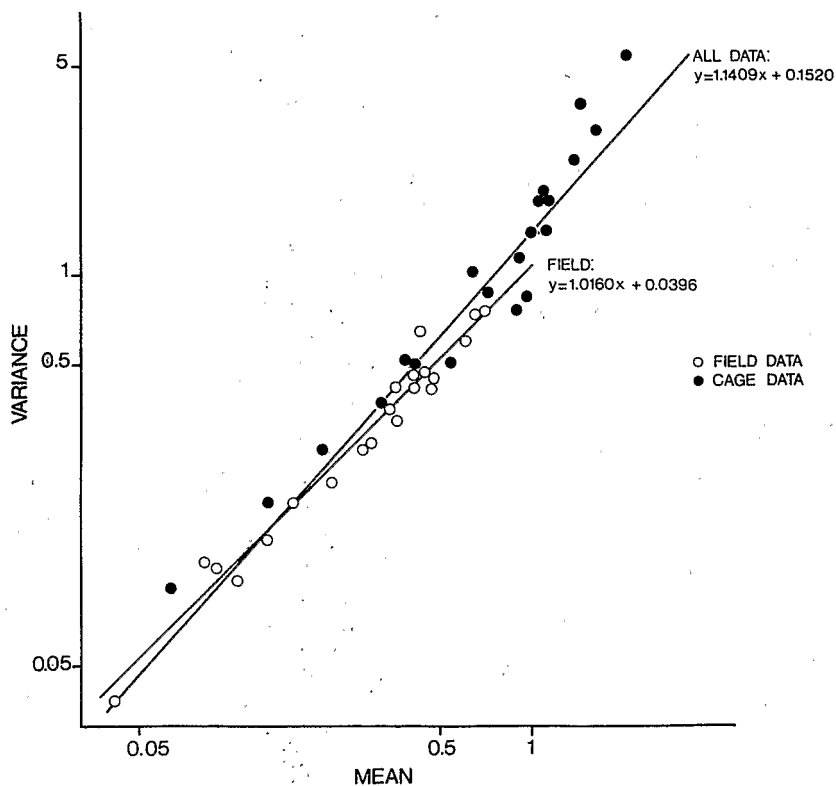S***: Significant at the 0.001% level.

Fig. 1. Relationship between the means and variances of *A. soccata* egg counts in 42 samples of 60–100 plants.

between field and cage data and no correlation between $I\delta$ and the mean. The regression of log s^2 on log $\bar{x}$ gives values of b of 1.016 ± 0.040 ($r = 0.985$) for field samples and of 1.123 ± 0.070 ($r = 0.964$) for cage samples (Fig. 1). These values are not significantly different and, when combined, give a b-value of $1.141 + 0.040$ ($r = 0.975$). The 95% confidence limits for this value being 1.060 and 1.221, eggs may be considered as randomly distributed, with a slight aggregation in cage samples at higher densities.

DISCUSSION

A. soccata egg distribution, as shown by various dispersion indexes and also by the comparison of observed and theoretical distributions is, under laboratory and field conditions, random or slightly aggregated; aggregation starts being detectable when the egg density reaches unity. In many insects [PRICHARD (1969); BARDNER and LOFTY (1971) for Diptera: TAYLOR (1961) for other insect orders], no sign of the existence of an oviposition deterrent could be brought to light; females do not seem to have any means of selecting their oviposition sites and therefore place their eggs at random among the available shoots. In the case of the sorghum shootfly, the presence of an oviposition-deterring pheromone results in the need for another explanation. A first hypothesis is that the effects of the pheromone are limited in time either because of volatility or water solubility; in that case, some time after having lost their attractiveness because of the presence of an egg, plants would recover their susceptibility and become capable of again receiving a second egg. The other hypothesis is that the effects of the anti-oviposition pheromone are masked by the presence of other stimuli which, under certain circumstances, may override the deterrent effect of the pheromone; such could be the case of factors pertaining to the plant like size, colour and turgescence which have a definite influence on the choice of the oviposition site by the female and may not easily be controlled in the laboratory, still less in the field.

The eggs of A. soccata are not laid at random on the different parts of a single plant: the lower leaf surface is much preferred to the upper one and the upper (last and before last) leaves receive more eggs than the lower ones (OGWARO, 1978). The pattern of distribution of eggs among plants is quite different: field and cage observations presented here are in very close agreement and show that the placement of eggs tends to be random or slightly aggregated rather than regular; this suggests that the site of oviposition by a female is little or not determined by the presence of other eggs. In the field, this type of distribution leads to a certain grouping of larvae which is much less favourable to survival than regular distribution of eggs. While an important proportion of plants remains uninfected, some plants bear two, three or more eggs, depending on the general egg density. As only a single first-instar larva is able to develop in a single shoot and as successful migration between plants is very unlikely, all larvae hatching from the additional eggs are destined to perish, either in the shoot itself or on the soil, during their search for an uninfested host.

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