Distribution of the snail *Biomphalaria glabrata*, intermediate host of *Schistosoma mansoni*, within a St Lucian field habitat

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A total of 6360 mud samples were obtained, in 62 collections made with an exhaustive sampling device, from banana drains on the West Indian island of St Lucia during fortnightly samplings over a 2½-year period. Analysis of counts of the snail Biomphalaria glabrata *from these samples showed that this species had a contagious distribution. This finding is consistent with other evidence that banana drains form a rigorous habitat for* B. glabrata. *Its distribution was more contagious than that of* Oncomelania quadrasi *in certain Philippine habitats and several species of aquatic snail in various African irrigation canals. The exact transformation for normalizing the snail counts for standard statistical techniques was* $z = x^{0.287}$ *but the more convenient cube root transformation is probably adequate. However, if too few snails are collected (15 or fewer per 100 samples) or if the frequency distribution of snail counts is discontinuous, with too many widely separated high frequency counts, neither transformation will be entirely satisfactory.*

Yeo (23), using the method of Taylor (20), demonstrated the aggregated distribution of several species of aquatic snail within an experimental irrigation canal in Tanganyika (now Tanzania). Mud samples were collected by a modification (1) of an exhaustive tube-sampling technique (9). The individual snail counts could be transformed to $y=x^{1/3}$ to permit normal statistical analysis techniques. However, Yeo warned that this transformation might not be applicable to snail counts from other habitats.

The same sampling technique was used by Sturrock (17) to study *Biomphalaria glabrata* in banana drains—one of the snail habitats on the West Indian island of St Lucia. The distribution of the species in that habitat is examined in the present paper.

MATERIALS AND METHODS

A detailed description of the study area and habitats is given by Sturrock (17). Banana drains remove excess rain water to prevent flooding of the fields and drowning of the banana plants. Parallel, earth-lined lateral drains, 0.5 to 0.7 m wide, 0.3 to 1.0 m deep, and 5 to 6 m apart, empty *via* similar but larger main drains into natural water courses. Depending on the terrain and rainfall conditions, these drains may contain standing or flowing water permanently or at irregular intervals.

Eight mud samples (1) were collected at each of 13 sampling stations at fortnightly intervals from March 1967 to June 1969. Exceptions were the first and third collections, when 32 and 88 samples, respectively, were collected. In total, 6360 samples from 62 collections were examined. Taylor's empirical method, as outlined by Southwood (14), was used to examine the data.

RESULTS

The frequency distribution of snail counts for the 6360 samples is shown in Table 1. Zero counts predominated, but there were some high counts. The counts do not follow a Poisson distribution, because the mean count ($\bar{x}$) was 0.5607 and the variance (s^2) was 6.5601. The cumulative frequency of the counts plotted on log probability paper (Fig. 1) gave a smooth curve up to 99.8%. Thus, although the counts do not follow a normal distribution, there is no immediate evidence of polymodality. The negative binomial parameter k was calculated from

$$N \ln [1+(\bar{x}/k)] = \Sigma [Ax/(k+x)]$$

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Table 1. Frequency distribution of snail counts among 6360 banana drain samples

No. of snails per sample *x*	No. of samples *f*	No. of snails collected *fx*
0	5441	0
1	387	387
2	169	338
3	93	279
4	62	248
5	38	190
6	31	186
7	18	126
8	25	200
9	13	117
10	10	100
11	8	88
12	11	132
13	4	52
14	8	112
15	5	75
16	3	48
17	2	34
18	5	90
19	4	76
20	4	80
21	1	21
22	2	44
23	1	23
24	2	48
25	2	50
26	3	78
28	1	28
29	1	29
35	1	35
39	1	39
41	1	41
53	1	53
56	1	56
63	1	63
Total	6360 (Σf)	3566 (Σfx)

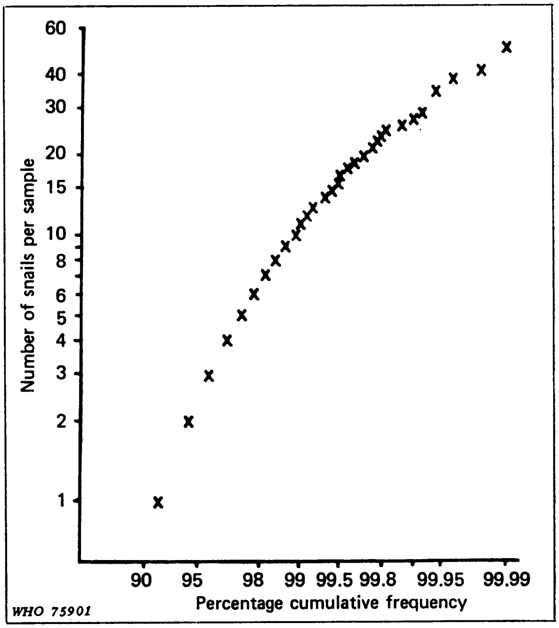

Fig. 1. Plot of $\log_{10}$ cumulative frequency of snail counts (fx) expressed as a percentage of the total number of snails collected ($\sum fx$) against the individual snail counts (x).

where N = the total number of samples and Ax = the sum of all the frequencies of sampling units containing more than x individuals (14). In this case $k = 0.0711$.

These was a linear relationship between $\log_{10} \bar{x}$ and $\log_{10} s^2$ where x and s^2 are the means and variances of the 59 collections that yielded snails (Fig. 2). The linear regression line was fitted by the method of least squares (13). The slope (b) was 1.426 ± 0.0491 at the $P = 0.95$ level of significance. According to Southwood (14), the exact normalizing transformation is $x^{0.287}$, calculated from $z = x^p$ where $p = 1 - \frac{1}{2}b$. The value calculated is intermediate between the two approximate transformations suggested by Southwood (i.e., the square root and the logarithmic transformations for values approaching 0.5 and 0, respectively), but is close to the cube root transformation used by Yeo (23).

The effects of both transformations on the relationship between x and s^2 are shown in Fig. 3 for the 59 collections illustrated in Fig. 2. The linear relationship is still discernible, but, for many of the data, the " variance is relatively independent of the mean " (14). However, two factors appear to limit the truth

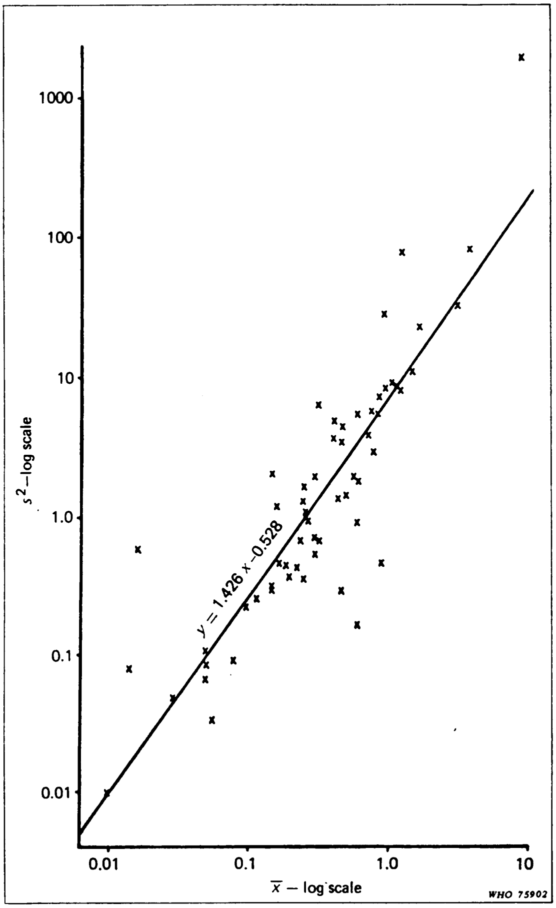

Fig. 2. Plot of $\log_{10}\bar{x}$ (mean snail count) against $\log_{10}s^2$ (variance for 59 collections yielding snails).

of this statement. It does not hold where the mean is very low—i.e., where $\bar{x}$ is less than 0.1 in both Fig. 3a and Fig. 3b, which represents total collections of fewer than about 15 snails in 100 samples. Examination of the original data from such collections shows that the majority of snail counts were in the range 0–2, which inevitably imposes an upper limit on the size of the variance.

A second factor became progressively more apparent as the number of snails collected increased. There tended to be a discontinuity in the frequency of snails per sample: clusters of high counts were widely separated from a smoother distribution of counts at the lower end of the scale. A relatively simple transformation, such as those used in Fig. 3, is unlikely to normalize this type of frequency distribution satisfactorily.

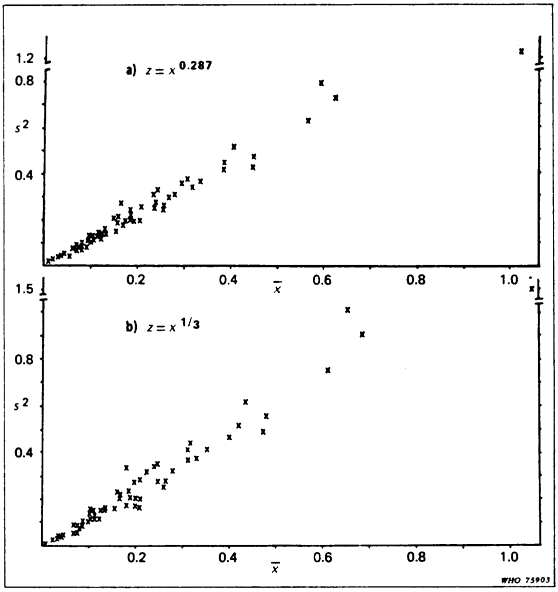

Fig. 3. Relationship of mean snail count ($\bar{x}$) to the variance (s^2) after normalizing the data to (a) $z = x^{0.287}$ and (b) $z = x^{1/3}$.

DISCUSSION

Accurate quantitative field data are needed to utilize fully the mathematical models currently being developed to study the dynamics of schistosome transmission and to design and assess control programmes. Such field data are difficult to obtain for a single species: the problems are compounded in schistosomiasis, in which three species (man, the parasite, and the snail), each with its own peculiar sampling problems, should be studied simultaneously.

Snails inhabit a variety of complicated habitats. Some authors have been fortunate enough to be able to use exhaustive sampling techniques without unduly disturbing specific habitats (1, 4, 6, 9, 10). More often, though, less reliable relative sampling techniques have been unavoidable (5, 17, 21, 22). Whereas the latter methods allow general trends to be studied and some attempt to be made at deriving population dynamics parameters (7, 16), little information can be obtained on absolute snail numbers.

It is generally accepted that snails are clumped in aggregated or contagious distributions within habitats. There is some evidence that this clumping is related to specific ecological microhabitats, such as certain plants (2, 9, 12). Alternatively, such clumping may be caused by social behaviour by the snails (11). However, little effort has been made to describe these clumped field distributions mathematically, even when exhaustive sampling procedures have been used.

A notable exception is the work of Pesigan et al. (9), who showed in the Philippines that *Oncomelania quadrasi* followed a negative binomial distribution in several habitats with $k = 1$, approximately. (The lower St Lucian value for k (0.07) suggests that *B. glabrata* had a more contagious distribution.) Later, Yeo (23) showed empirically that the snail counts from a Tanganyikan irrigation canal could be normalized by the cube root transformation. Hairston (4) used the same transformation, modified by adding 0.5 to each count to allow for zero values, for snail counts from irrigation canals in the Sudan and Egypt because it was simpler than more complicated transformations based on the negative binomial distribution. In fact, the addition of a constant to the raw counts is unnecessary for the inclusion of zero values when a power transformation is used: it is required only for logarithmic transformations. The similarity of snail distributions in these irrigation canals may reflect the homogeneity and similarity of this type of habitat. However, Yeo pointed out that other habitats might have different snail distributions, and variations in the slope (b) of $\log_{10} s^2$ on $\log_{10} \bar{x}$ might have ecological significance in defining the suitability of different habitats for snails.

In Tanganyika, $b = 1.29 + 0.08$; in St Lucia, $b = 1.426 \pm 0.049$. The latter figure is higher, probably significantly so, suggesting that *B. glabrata* is more contagiously distributed in the heterogeneous conditions of the banana drains than are other aquatic snails in the relatively homogeneous African irrigation canals.

In Yeo's data, the exact normalizing transformation ($x^{0.355}$) is not significantly different from the more convenient cube root transformation ($x^{1/3}$) that may be used prior to the application of robust statistical techniques such as the analysis of variance. The same is probably true for the St Lucian data but, as shown in Fig. 3, the cube root transformation is less effective than the exact transformation in reducing the dependence of the variance on the mean.

The contagious distribution of *B. glabrata* undoubtedly reflects primarily the heterogeneous nature of the banana drains. At any time, except during floods, conditions vary widely, ranging from dry, sun-baked drains, devoid of vegetation and extremely unsuitable for snails, to shaded drains with lush vegetation and gently flowing water in which snails thrive. These conditions, moreover, are not constant and one drain may revert from one extreme to another in a quite short time, owing mainly to seasonal variations in rainfall but also to periodic cleaning of the drains in routine banana husbandry. In adverse conditions many snails die, but those that survive—often by aestivation (15)—can repopulate the habitat explosively when conditions become favourable again, because of their high intrinsic rate of natural increase (18). Nevertheless, conditions in the drains are on the whole very harsh for *B. glabrata*, as was borne out by field observations (16, 17): hatchling and juvenile snails were relatively less common than in other habitats, birth rates were generally low, and death rates were frequently high.

How *S. mansoni* transmission is affected by the aggregated distribution of the snails depends on the pattern of human contact with the habitat. On St Lucia, human contact with banana drains is low and sporadic and, judged by snail infection rates, this habitat is one of the least important in *S. mansoni* transmission. However, it is possible, in other habitats with close human contact, that aggregation of the snails may potentiate transmission. Thus, the local situation must be taken into account in mathematical models, such as that of Goffman & Warren (3), in which prominence is given to the role of the snails.

It might be thought that the harshness of the environment would favour snail control by molluscicides. Paradoxically, the reverse was the case in the St Lucian banana drains. High snail kills were possible where conditions were favourable to snails, because adequate water was present to allow the molluscicide to work. In damp or dry drains, however, aestivating snails were often immune to the molluscicide and rapid repopulation by the survivors was possible when conditions became more favourable. In such circumstances, a molluscicide control programme must incorporate a stringent surveillance–treatment element to prevent a post-treatment resurgence of the snail populations. After several years of such a programme on St Lucia, large colonies—though scarcer than before—were still being detected in the banana drains (19). These colonies probably played little part in transmission, but they were still important because they formed a reservoir of snails to reinvade other adjacent habitats.

One method of assessing the effectiveness of molluscicising is to measure the percentage mortality caused among the snails (4). Such data, in conjunction with data on changes in incidence among the human population, might allow the quantitative estimation of the break point in transmission postulated by Macdonald (8). The cost–effectiveness of molluscicising would then also be calculable. Because of the clumped distribution of the snails, the use of raw snail-counts is inappropriate and, possibly, dangerously misleading. Suitable transformations must be used (4, 23).

The transformations illustrated in Fig. 3 would probably suffice for many of the data, but the limitations already noted should not be overlooked. The precontrol assessment will probably sample large snail populations and, if the frequency distribution of the snail counts is discontinuous, these transformations will be inappropriate. If the molluscisiding has been successful, then post-application snail counts will be very low. Again, the counts may not be adequately normalized by the transformations shown above. A further complication, to some extent suggested by qualitative rather than quantitative data obtained in St Lucia (19), is that the distribution of the snails may be altered by the application of molluscicides. In this case, the same transformation is unlikely to be appropriate for pre-control and post-control snail counts.

In fact, no attempt was made to estimate the total pre-control snail population in the banana drains on St Lucia, because the sampling stations had not been selected to represent proportionately the different types of drain present. To design such a sampling programme for 1000 km or more of drains in which conditions are variable and unstable would have been an enormous and, probably, impossible undertaking. Similarly, no assessment of the size of the post-treatment snail population was attempted and the efficiency of the programme was judged primarily by the effect on the incidence of human infections

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RÉSUMÉ

DISTRIBUTION DU MOLLUSQUE *BIOMPHALARIA GLABRATA*, HÔTE INTERMÉDIAIRE DE *SCHISTOSOMA MANSONI*, DANS UN HABITAT AGRICOLE À SAINTE-LUCIE

Dans l'île antillaise de Sainte-Lucie, *Schistosoma mansoni* est transmis par le mollusque *Biomphalaria glabrata* qui a notamment pour habitat le système de drainage des bananeraies. Utilisant une technique complète d'échantillonnage, à intervalles de 15 jours, on a recueilli, entre mars 1967 et juin 1969, 6360 échantillons dans 13 stations de drainage. Le résultat prédominant des numérations était nul mais le nombre moyen de mollusques par échantillon ($\bar{x}$) était de 0,5607, avec une variance (s^2) de 6,5601. La distribution était fortement groupée; pour une distribution binomiale négative, la valeur de k était de 0,0711. Parmi les 59 collectes bimensuelles qui ont fourni des mollusques, il y avait relation linéaire entre le $\log_{10} \bar{x}$ et le $\log_{10} s^2$ avec une pente de 1,426 ± 0,0491 au niveau de signification $P = 0{,}95$. La transformation exacte en vue de normaliser les nombres trouvés aux fins des techniques statistiques traditionnelles était: $z = x^{0,287}$ (ou $z = (x + 1)^{0,287}$ pour tenir compte des résultats nuls) mais on peut se contenter de la formule plus commode $z = (x + 1)^{1/3}$. Toutefois, il n'est pas possible d'obtenir une normalisation satisfaisante si le nombre de mollusques recueillis est inférieur à 15 pour cent échantillons ou si la distribution de fréquence des nombres trouvés est discontinue, avec un grand nombre de hautes fréquences très espacées. Il semble donc que la distribution de *B. glabrata* dans le système de drainage des bananeraies de Sainte-Lucie soit plus groupée que celle de mollusques semblables dans un certain nombre de canaux d'irrigation

africains et dans divers habitats des Philippines. Cette observation correspond au caractère hétérogène des systèmes de drainage des bananeraies et au fait qu'ils constituent un habitat très pénible pour *B. glabrata*. Il est important d'obtenir ce type de données quantitatives afin de pouvoir utiliser efficacement les modèles mathématiques, qui sont en préparation pour l'étude de la dynamique de la transmission, ainsi que pour la conception et l'évaluation de programmes de lutte.

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