

Most of these assumptions could be broadly justified by reference to the literature. The observations made by Pilson and Pilson on the feeding behaviour of Glossina morsitans deserve the most careful consideration, since they appear to run counter to commonly accepted views of the distribution of this species in relation to vegetation. Most of our ideas about this aspect of tsetse biology are based on knowledge of the distribution of a small fraction of the whole population, namely males in what I have described as the sexual appetitive phase of the hunger cycle ("sexual males" for short). This constitutes a serious limitation, but it is one that we have learnt to live with, and the suspicion that our ideas may be completely wrong comes to us only during periods of mental depression. But the observations under consideration lend substance to just such a suspicion, and it is for this reason that they are of foremost importance.

It has, I think, been generally considered that in many parts of Rhodesia, the riverine vegetation forms a dry season "retreat" for the tsetse population, since at this time of the year AD's are very much higher in or near this vegetation type than they are in the general woodland. On this view one would expect a correspondingly high density of other sections of the population in riverine vegetation, yet there is no marked difference between vegetation types as regards the female feeding catch, and the male feeding catch in the riverine is little more than twice that of the open woodland. To bring these observations into line with the traditional view it would have to be assumed that although the riverine vegetation serves as a dry season habitat, flies of both sexes disperse from it in search of food. But if this were so one would expect the feeding density to fall off with distance from the river, and of this there is no sign in the results under discussion. On this view, too, it would have to be assumed that flies could find their way back to the river from a distance of several miles in the absence of any significant gradients of temperature or humidity. This is to credit the species with superlative "homing" ability, for which there is no shred of independent evidence. Furthermore, such information as exists concerning the rate of dispersal of tsetse flies suggests that it is usually limited to distances of the order of 200 yards per week.

The most striking evidence, however, against the view that riverine vegetation constitutes the dry season habitat is furnished by pupal distribution. Dr. Phelps has kindly allowed me to examine his data from Lusulu, and the figures show quite clearly that only a small fraction of total deposition occurs at the river, and the proportion of pupae found in riverine vegetation does not increase to any great extent with the onset of the hot dry season.

In view of these considerations it seems to me necessary to abandon the idea that riverine vegetation constitutes a dry season "retreat" for the tsetse population as a whole. The evidence surely suggests that concentration onto this vegetation phase is limited largely to the sexual male; and the observed increase in female percentage in the general woodland and decrease on the river would follow as an inevitable consequence of such concentration. The mechanism of concentration could be a simple difference in the velocity of dispersal in different vegetation types during this phase of the hunger cycle; where suitable resting sites are abundant, as they would be in riverine vegetation, the rate of movement could be imagined to be slower than when resting sites are few and far between. It seemed worth while to determine whether a mechanism of this type would indeed account, in broad terms at least, for all of the observed facts, and a model was accordingly constructed on the basis of a few simple assumptions:-

1. The proportion of females to males is 60:50
2. The duration of the hunger cycle is the same in males and females
3. The relative duration of resting and active phases in the female hunger cycle is 3.5:1.5; in the male hunger cycle it is 1:4, with the active phase divided into two equal parts, one of sexual and one of appetitive behaviour and one of feeding behaviour.
4. In the presence of a host animal (as under the conditions of the field observations) 25% of the population is always on the host.

Most of these assumptions could be broadly justified by reference to the literature, but chapter and verse have not been given since the values chosen have little influence on the fundamental properties of the model; they serve merely to fix the general level of the female percentage in a feeding catch.

6. The direction of dispersal of males and females is random with respect to vegetation
7. The velocity of dispersal is independent of vegetation except for the sexual male, in which it is inversely proportional to the density of "suitable" resting sites.

On the basis of this set of assumptions, the distribution of population elements between vegetation phases differing with respect to the density of resting sites can be calculated, and Fig. 1 shows the expected percentage of females in riverine vegetation and in open woodland as a function of the velocity ratio, that is, of the number of times the dispersal velocity of sexual males in open woodland exceeds that in riverine thicket.

The velocity ratio would be expected to be low during the rains when the surrounding woodland is in full leaf, and to increase progressively through the cold dry season to a maximum during the hot dry season. According to the model this should result in a fall in the riverine female percentage from about 40 in the rains to 24 in the hot dry season, which is in good agreement with recorded values of 39% in the rains, 30% in the cold dry and 25% in the dry hot season. At the same time the woodland percentage would be expected to rise from about 48% to 54%; unfortunately no data are available for the rains, but a change in the right direction is shown by mean values of less than 50% for the cold dry season, rising to 54% (Paper I) and 63% (Paper II) in the hot dry season.

Fig. 2 shows that during the rains the apparent density in riverine vegetation should be little greater than that in open woodland, but that with the advance of the dry season riverine AD's may be many times the woodland level. Male feeding densities on the river, on the other hand, never rise to values more than 3-4 times the woodland level in accord with the observed facts, while female feeding density (not shown on the graph) remains equal in woodland and riverine at all seasons, as observed.

Another feature to which Pilson and Pilson draw attention is the early flushing of Brachystegia woodland as compared with mopane, a difference which seems to be reflected in a corresponding difference in female percentage which averages 68 for mopane and 54 for Brachystegia. In this case the areas involved may be considered to be roughly equal in extent, and under these circumstances quite a small difference in dispersal velocity may give rise to a substantial difference in female percentage, as shown in Fig. 3. The observed difference of 15% would occur if the dispersal velocity in leafless mopane were no more than 3 times what it is in flushed Brachystegia.

In general terms it would seem that the facts in the case - the observed differences in female percentage in different vegetation types and from season to season, the observed differences and changes in male feeding density and apparent density, the constancy of female feeding ratio between different vegetation types - all can be accounted for in qualitative and quantitative terms on the basis of the proposed model. It is not claimed, of course, that such a simple model can furnish anything like a complete description of a tsetse population; no account has been taken of the relation between game and fly, for one thing; nor is it easy to believe that dispersal is completely random with respect to vegetation, but this does not mean that there may not be an important random element superimposed on directional components involved in the "ambit" effects described by Jackson. Indeed, the only thing to do with a model of this kind, once having seen how it behaves, is to forget it and put the case in far more general terms. Which is to say simply that the results obtained by a variety of survey methods - fly rounds, bait catches, pupal surveys and resting fly censuses - find a common interpretation on the basis that sexual males, for whatever reason and by whatever mechanism, make special use of, or are especially attracted to, or tend to be confined or

the rise in female percentage which often follows selective application of insecticides would be a natural outcome of the heavy male mortality which would be expected to occur; indeed, on the basis of this interpretation the spraying of an equivalent area in random strips might be expected to produce equally good results. Again, the failure of most discriminative clearing schemes is hardly surprising if this view of population structure is accepted; all such clearing does is to prevent the usual build-up of sexual males in the treated areas. The massive fall in A.D. which usually follows is not indicative of a general population collapse, but simple indicates that the males are more widely dispersed; and populations can often be found subsisting quite happily in regions adjacent to the clearings, e.g. Urambo, Ngara etc. This underlines the possibility that fly rounds may not be the most suitable indication of population trends following control operations of this type.

Whether or not the views set out above prove to be acceptable it cannot, I think, be denied that the results on which they are based are of the utmost importance, and that every effort should be made to confirm and extend them. No general interpretation of the relation between tsetse and vegetation which fails to take this aspect of the situation into account can pretend to lasting validity.

E. Bursell

The most striking evidence, however, against the view that tsetse populations are limited by the dry-season habitat is furnished by pupal distribution. It is clear from the data of Bursell (1954) that the proportion of pupae deposited in the dry-season habitat is very small, and that the proportion of pupae deposited in the dry-season habitat is very small, and that the proportion of pupae deposited in the dry-season habitat is very small.

In view of these considerations it seems to me necessary to consider the view that tsetse population fluctuations are due to a "bottleneck" in the dry-season habitat. The evidence clearly suggests that concentration of the population in the dry-season habitat is limited largely to the sexual males; and the observed increase in female percentage in the general woodland and decrease on the river would follow as an inevitable consequence of such concentration. The mechanism of concentration would be a simple difference in the velocity of dispersal in different vegetation types during the phase of the hunger cycle when dispersing males are abundant, as they would be in riverside vegetation, the rate of movement could be imagined to be slower than when dispersing males are few and far between. If assumed with little to detract from its plausibility, of this type would indeed account, in broad terms at least, for all of the observed facts, and a model was accordingly constructed on the basis of a few simple assumptions:-

1. The proportion of females to males is 40:50
2. The duration of the hunger cycle in the male is twice that in the female
3. The relative duration of resting and active phases in the female hunger cycle is 1.5:1.5; in the male hunger cycle it is 1:1, with the active phase divided into two equal parts, one of wandering and one of feeding behaviour.

