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TSETSE CONTROL IN RELATION TO WILD LIFE  
CONSERVATION

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A review of the results obtained with current methods of tsetse control suggests that treatment with residual insecticides constitutes the most promising line of attack. But it seems likely that this method may not be applicable under all conditions and for this reason consideration needs still to be given to the development of other methods of control. Experience in East Africa shows that discriminative clearing is a poor alternative; game destruction on the other hand, is a method which is theoretically sound and in practice effective, at least in areas where it can be effectively carried out. Attention should therefore be directed towards a reconciliation between the apparently diametrically opposed requirements of game destruction and wild life conservation, and it is the purpose of the present paper to show that such a reconciliation is, in some measure, possible.

Apart from the theoretical soundness of game destruction as a means of control, there is another reason why an attack on the food supply of the tsetse fly should be a promising approach. Because there is evidence that the food supply may be a controlling factor under natural conditions. In other words, that tsetse populations are at all times hard pressed for food. And this means that even a slight amount of interference in the direction of reducing available food should have a corresponding effect on population density; should reduce the expectation of life, hence the reproductive potential and hence the equilibrium density of the population.

With regard to the expectation of life of tsetse flies we have a great deal of reliable information, and we know beyond a reasonable shadow of doubt that in the field they don't live as long as they ought to. The mean life of flies in the hot dry season may be as little as 2 - 4 weeks; but in the laboratory the mean age of populations maintained under conditions which we are sure are markedly suboptimal, it is 14 weeks or more. Clearly the short life span of flies under natural conditions cannot be ascribed to death from old age. Some factor or complex of factors operates to reduce drastically the life span of flies in the field; and starvation is, without question, an important element in the complex. What other potential causes of death might contribute to the effect? The only two candidates which present themselves at first sight are predation and parasites. Unfortunately no quantitative studies are at present available concerning the importance of these in relation to adult mortality, but the consensus of opinion seems to be that they play only a minor role, if any, in the control of tsetse numbers.

So we may, on the basis of these considerations, and for the sake of argument, if nothing else go so far as to suggest that starvation is not only an important cause of death under natural conditions, but that it is, for practical purposes the only cause of death. That, in fact, the whole problem of tsetse population dynamics should be seen in terms of a balance of two opposed rate processes:

- (a) the rate of utilisation of food reserves, and
- (b) the rate of replenishment of food reserves or, as we would say, the frequency of host encounter.

If (a) is high in relation to (b) then a high proportion of flies will exhaust their food reserves before they have a chance to find another meal, and the expectation of life in the population will be low; if (a) is low in relation to (b) most of the flies will find food before their reserves are exhausted and the expectation of life will be high.

If we are prepared to accept this view, at least in general principle, then we can go one step further; for we can construct a simple mathematical model of a tsetse population and investigate a few of the quantitative aspects of the situation. We need not go into detail about how this is done, only to say that if we know, and we do know roughly, how long a tsetse fly lives under given conditions of temperature, from the time it is willing to take a meal until it dies of starvation; then we can work out its expectation of life for any given level of what we might call host encounter probability. In other words, we can balance the two opposed rate processes, (a) and (b) in quantitative terms. The position can be expressed as a graph of host encounter probability against expectation of life, and the picture we get for a Glossina morsitans community in the early dry season is shown in Fig. 1.

A host encounter frequency or probability (P) of 0.1 means that the chances of seeing game, or rather of finding a suitable host, on any one day is 1 in 10; in other words, that such a host is encountered on the average one day in 10. With a feeding span of 3 days, which is about right for that time of the year, we get a hyperbolic curve extrapolating to 4 days, which is the time that a newly emerged fly would live without a blood meal, i.e. when P is zero. On the other side the curve is asymptotic at a P of 0.33; because with 3 days to feed the probability of finding a suitable host would be 0.333 plus 0.333 plus 0.333 or 1.0, in other words, flies would always find a host before their reserves are exhausted. In actual fact, of course, the curve doesn't go to infinity, but levels off at the mean age to which flies can attain before they die of old age - probably about 100 days or so. But this part of the graph is not very relevant because the situation which it represents doesn't seem to occur in nature.

What we are interested in is the sort of level of life expectancy which characterises the natural population, and we can make a fairly good guess at what this is. Because we know that at this time of the year the population is just about maintaining itself at a steady level, neither increasing nor decreasing. And in order to maintain itself each female in it must live long enough to produce one female and one male pupa; and at this time of the year it takes about 30 days to achieve this replacement. And referring to Fig. 1, it can be seen that a life expectancy of 30 lies on the steep part of the curve; which means that under the conditions which characterises this population a very small shift in P will produce a large shift in life expectancy. If we could reduce the host encounter probability from 0.29 to 0.26 we should reduce the expectation of life by a third; and if the average life falls to 20 days a female will only just be able to produce 1 pupa in its life: in other words, the population will fail to maintain itself. And if we can keep the expectation of life at this level the population will decline and decline and decline until it eventually dies out.

This is just another way of saying what has already been inferred on general grounds, namely that even slight interference with the game should produce a corresponding effect on the tsetse population. But it does bring us up against some rather disturbing anomalies. Because granted the assumptions which we have made, it means in the first place that for a population of G. morsitans during the early dry season the probability of host encounter is 0.3, whereas anyone who has worked in the sort of environment under consideration will swear, and rightly, that he doesn't have to spend 3 days in the field in order to see a game animal. Secondly, it tells us that the presence of a shooting gang in the area should almost immediately make its presence felt; whereas it is general experience that you have to go on shooting for a long time before things start happening, if ever. These two anomalies are in all probability to some extent related.

The first point is that perhaps the game that one sees when one walks about the bush, the game that the game scout shoots at the beginning of a shooting campaign, may not in fact be the sort of game that a tsetse fly considers a suitable host. and that this is so we have abundant evidence, because in recent years a method has been developed by Dr. Weitz which enables us by serological means to determine exactly what kind of animal a tsetse fly has fed on.

This kind of discrepancy between common sense, as it were, and fact, was particularly striking in a place called Shinyanga. There we had a lot of information about what animals the local tsetse flies fed on, from studies covering a period of years. And it turned out that warthog was the exclusive favourite at all times; between 90 and 96% of all meals taken by tsetse flies in the area were off warthog. Now I won't maintain that warthog were scarce in the area, because they were not. But you didn't see a warthog every time you spent a day in Block 9, the local habitat of the fly; what you did see every single day were dik-dik and impala; but virtually not a single meal of the many thousands which were sent to Dr. Weitz had been taken off dik-dik or impala.

There can be little doubt that the same sort of effect may account to a large extent for the delayed action of shooting operations; and for the apparent anomaly that while you see game every time you visit an area the tsetse flies see a suitable host only once in three days. What you see and what you shoot is just not what the tsetse fly eats.

As for the shooting there is, of course, another factor - many of the favoured hosts of tsetse flies are social by nature; warthogs, for example, are often, if not usually, seen as a family group; and to shoot one or two of such a group does not affect the tsetse fly, it can still get a meal off the others. You do not reduce the host encounter frequency until you shoot all of the warthogs in a group.

But why is it that tsetse flies seem to have a preference for certain types of animal; why will a tsetse fly all but starve to death before it will take a feed off a herd of impala or a couple of dik-dik or a zebra which walk right past them? This is the problem so strikingly posed by Dr. Weitz's results, a problem of game destruction, yet one which has received virtually no attention.

A few things bearing on this problem have in fact been

not enough to take a warthog with you; in spite of the fact that warthog is the all time favourite, the presence of a warthog in the catching party has no, or practically no effect on the catch you make. It is still predominantly one of flies which are not yet interested in feeding. It is clear that the feeding of tsetse flies is not just a question of having the right kind of animal; you seem to have to have the right kind of animal doing the right kind of thing in the right kind of place perhaps at the right kind of time. And we have in fact some preliminary information that two elements are of particular importance to the feeding reaction - one is quiescence and the other is shade. For an animal to constitute a suitable host it has to be lying up under the shade of a tree or in a clump of thicket. An object moving about in the sun does not seem to constitute an effective stimulus to feed; unless it is a very large one, such as a lorry or an elephant.

Now if we look at the so-called preferences of tsetse flies for different kinds of animal in the light of these findings, some kind of correlation is evident. For on the basis of the analysis of 1000s of blood meals animals have been divided into two main categories:

- (a) those which are commonly or always fed on, and
- (b) those which are rarely or never fed on.

In the first category (see Table 1) we find predominantly animals which spend a great part of their time lying up under shade; such as warthog, rhino, man, reedbuck, buffalo, kudu, bushpig and bushbuck. The only exceptions are elephant and giraffe, but here we could perhaps invoke the factor of size to account for their presence in the "bitten" category.

In the second category we have species which do not lie up much; like eland, duiker, baboon, impala, monkey, birds, hartebeest, topi, zebra, wildebeest, or if they do, lie up in places not visited by tsetse flies, like hyena and porcupine.

Such broad correspondence between the feeding pattern of tsetse populations and the habits of game suggest very strongly that a study of the behaviour of game animals would be of the utmost importance in relation to the problem of tsetse control. But the kind of information that we want if we are to interpret the population dynamics of the tsetse fly in terms of host encounter frequency is just not available; and the reason is not far to seek. Because the sort of thing we want to know, the proportion of time a given species spends in different types of activity for instance, is not something which is readily amenable to systematic study. Such an investigation would be more in the nature of a vocation; because we want to know about the intimate life of the animal, which means that we have got to live and breathe and think with it. And this calls, in each species, for a lifetime of affectionate study.

But it seems to me that some of you have perhaps just the requisite kind of affection for a given species of animal, and that you live under conditions where you are in a position to make constant observation of the species behaviour. And what I have tried to do this morning is to emphasize how desperately we need carefully recorded observations of the behaviour of game animals if we are to get anywhere with the interpretation of tsetse biology. How much time is spent in different parts of the habitat at different times of the year; how much time is spent feeding,

Table 1.

The relative importance of different animals as sources of food  
for Glossina morsitans.

(from Weitz, B., & Glasgow, J.P. (1956). Trans Roy. Soc. trop.  
Med. & Hyg., 50, 593 - 612).

Host.	% of feeds derived from the different species.
Warthog	45.9
Man	6.9
Kudu	5.6
Buffalo	4.8
Roan	4.1
Ox	4.1
Bushpig	3.9
Giraffe	3.7
Rhinoceros	2.9
Bushbuck	2.6
Reedbuck	2.3
Birds	2.3
Elephant	2.2
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Baboon	1.6
Eland	1.3
Duiker	1.1
Monkey	0.8
Impala	0.8
Waterbuck	0.7
Sheep	0.6
Dogs	0.6
Hyaena	0.3
Cats	0.3
Porcupine	0.3
Donkey	0.3
Hartebeest	0.0
Zebra	0.0
Topi	0.0
Hippopotamus	0.0

Dogs include bat-eared fox, wild hunting dog and jackal.  
Cats include lion, leopard and cheetah.

sleeping, just thinking. Now often is water visited and so on and so on. With this kind of information we might ultimately be able to interpret the feeding pattern of a tsetse population, to say not only that 70% of the feeds are taken off warthog and 20% off bushbuck but why.

And if we could offer some kind of explanation in terms of what one might call the dynamic game pattern, one would then be in a position to tackle the problem of control in an intelligent fashion. Because we could say, perhaps, here we have a population whose mean expectation of life is 40 days, say. Since the time allotted for feeding in each hunger cycle is, say, 3 days therefore the host encounter probability is 0.31; in order to reduce the expectation of life to a level where the population can no longer maintain itself we must reduce the life expectation to 20 days which means that we must reduce the probability of host encounter to 0.26; and in order to do this we must remove, say 20% of the warthog units and 10% of the bushpig units. In other words, we would be in a position to say not game destruction, but game cropping; or even the control of tsetse flies by the utilisation of indigenous mammals.