THEORETICAL ASPECTS OF THE CONTROL OF
GLOSSINA MORSITANS BY GAME DESTRUCTION

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The use of game destruction as a method of tsetse control has always been highly contentious. It is naturally repugnant to wild life conservationists, and at a time when the preservation of wild life resources is a live issue in the context of African ecology, the few tsetse control departments that still practise game destruction are likely to have the full force of public opinion ranged against them. The fact remains, however, that game destruction can be an extremely effective method of control, and it is based on impeccable theoretical considerations; for it is known that vertebrate blood constitutes the only food and drink of tsetse flies, and it must follow that destruction of vertebrates will inevitably lead to the elimination of the tsetse population. That it does, in fact, do so has been unequivocally established by an experiment carried out in Shinyanga in the 1940's (Potts and Jackson 1952), and the results of that experiment have been verified by the experience of tsetse reclamation departments in many parts of Africa. If there had been other and equally effective means of control at our disposal, there would certainly be a good case for avoiding a method as drastic as game destruction; but in my opinion there are at present no satisfactory alternatives. Discriminative clearing has proved to be theoretically unsound (Pilson and Pilson 1967; Bursell 1966) and, in practice, of limited value. Insecticides are only useful in local situations and as a means of temporary alleviation; they are unlikely to prove effective in pushing back an extensive tsetse front, because of the tendency for treated areas to be re-invaded. The method of sterile male release, possibly coupled with one or two applications of insecticide, shows considerable promise (Dame and Ford 1966), but its development is still in the very early stages, and even if it does prove a success, it will be many years before it can be brought to the point of large scale application. In view of these considerations it would be irresponsible, at this stage, to dismiss the one sure means of defence against the tsetse. Consideration should rather be given to the possibility of resolving the apparent antithesis between the requirements of wild life conservation and of tsetse control, and it is the purpose of the present paper to bring forward a few considerations which might be relevant in this context. These considerations will be highly speculative, since the sort of evidence which they would require for their detailed substantiation is not available at this time. I do not imagine, therefore, that they can hope to gain general acceptance, but they may serve to draw attention to the urgent need to explore in detail the relation between the tsetse and its host, a field of study which has been almost entirely neglected despite the fact that it may well prove to hold the key to effective and acceptable tsetse control.

Very little is known about the relationship between host and fly, beyond the important fact established by Weitz and his collaborators (e.g. Weitz and Jackson 1955, Weitz and Glasgow 1956, Glasgow *et al* 1958) that certain species of host animal are commonly fed on by testse flies, others hardly at all. The precise mechanism by which host animals are located

at the end of successive hunger cycles is not known, but since starvation appears to be a common cause of death under natural conditions (Bursell 1961), it is clear that a substantial proportion of tsetse flies exhaust their food reserves before they succeed in their search for a suitable host. In view of this it may be legitimate to regard the population dynamics of tsetse flies as involving in essence a balance between two opposed rate processes, namely:

     (i) the rate of utilisation of food reserves, and

     (ii) the rate of replenishment of food reserves, which may be described as the frequency, or the probability, of host encounter.

If (i) is high in relation to (ii), then a high proportion of flies will exhaust their food reserves before they have a chance of replenishment, and the expectation of life in the population will be low; if (i) is low in relation to (ii), the majority of flies will succeed in feeding at the end of each hunger cycle, and the life expectancy will be high in the population.

The work of Jackson (1954) and of Vanderplank (1947) enables estimates to be made of the duration of the hunger cycle (i.e. the interval between successive blood meals), and of the feeding span (i.e. the time that a tsetse fly can live from the moment that it starts to search for food until it dies of starvation). On the basis of such estimates it is possible to express the balance between food utilisation and food replenishment in quantitative terms, and a relationship can be derived between the daily probability (P) of host encounter (i.e. the chance that a tsetse fly has of meeting a suitable host on any one day) and the average expectation of life. The method of calculation is described in Appendix I, and Fig. 1 shows curves appropriate to different seasons of the year. Curve (a) depicts the expected relationship between P and longevity during the hot season, with temperatures averaging about 30°, and curve (b) applies to the cold season with mean temperatures in the region of 20°.

The curves extrapolate to 3 and 6 days respectively at zero probability, since at this level flies emerging from their pupae would have no chance of finding food, and would simply starve to death. At the other extreme, both curves tend towards infinity as the probability of host encounter for the feeding span approaches 1.00. At this point flies would always succeed in finding a host before their reserves ran out, and they would theoretically live to become infinitely old. In reality, the curves would level off at the mean age to which flies attain before they die of old age. At a temperature of 25° this would be about 100 days for females (Phelps, personal communication) and both curves have been discontinued at this level.

The argument which has been developed here obviously constitutes an over-simplification of what must in reality be an extremely complex situation. It is based, for instance, on the assumption that starvation is the only cause of death in a tsetse population, and this is certainly not the case, though it may well be the most important one. Secondly, it treats host encounter as if it were a simple environmental factor, whereas in fact it represents a variable interaction between the insect and its environment; under a given set of conditions the precise value of P would depend in large part on the activity of the tsetse, in the sense that if a greater amount of time were spent in hunting during later parts of the feeding span, the encounter probability would be correspondingly increased. But such considerations do not alter the fact that, since there is a fixed duration of the feeding span (although it may not be accurately known), and
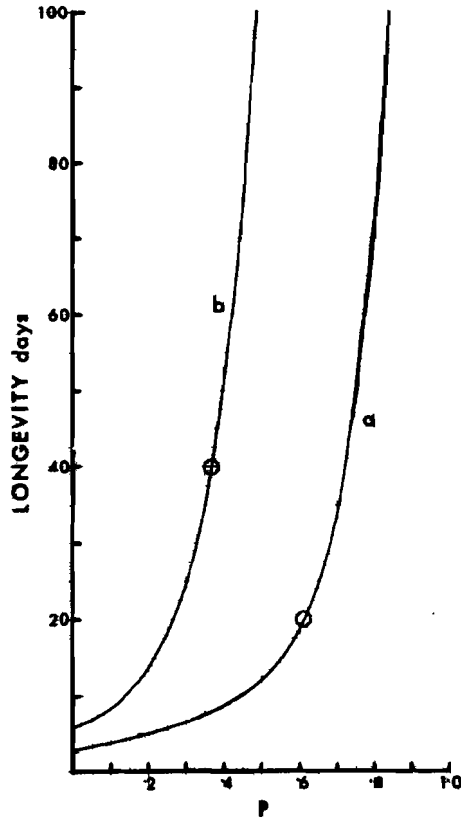
FIGURE 1

The relation between host encounter probability (P) and longevity (days) in populations of tsetse fly during the hot (curve "a") and the cold (curve "b") season. Replacement thresholds have been marked as open circles on the curves. For further explanation, see Appendix I and text.

since the probability of host encounter during that feeding span will have a finite value less than 1.0 (otherwise flies would not die of starvation), it follows that the relation between host encounter probability and life expectation is likely to take the general form of the curves shown in Fig. 1.

The question as to the position which a natural population might occupy on the co-ordinate grid of Fig. 1 is one which may be approached from the point of view of population dynamics. It appears that tsetse populations tend to be relatively stable in the long term but show consistent short term fluctuations related to the seasons of the year (Glasgow and Welch 1962, Jackson 1948). For a population to maintain itself at a steady level, females must live long enough to produce at least one female pupa and, since the pupal sex-ratio is 1:1, this means that at least 2 pupae must be produced—more if allowance is made for mortality during developmental stages. Under hot conditions (30°) the time taken by a female to produce

two pupae would be about 20 days, and under cold season conditions (20°), 40 (Jack 1939). These "replacement thresholds" have been marked on the curves in Fig. 1, and it can be seen that they correspond to P-values of between 0.4 and 0.6. A value of encounter probability in this region would therefore satisfy the conditions of a natural population in so far as it would give the appropriate seasonal fluctuations about a steady long term level. During the hot season, average life expectancy would be below replacement threshold, and population densities would decline; during the cold season longevity would exceed replacement threshold and densities would increase. The corresponding estimates of longevity are not inconsistent with such information as is available on the survival of females under natural conditions. Jackson (1940, 1944 and 1948) has shown that life expectancy at the peak of the hot season may be no more than a few weeks, while during the cold season death ceases to be random with respect to age, suggesting that a proportion of flies may at this time live long enough to die of old age.

It would seem, then, that an encounter probability in the region of 0.5 might be applicable to the natural situation, implying that, on average, a period of 2 days would have to be spent before a suitable host is encountered. From the point of view of the human observer this would betoken a rather sparse population of game, but there are two factors which need to be taken into consideration in this context. In the first place it has been shown that the feeding activity of *Glossina morsitans* may, during most parts of the year, be restricted to a few hours after dawn and before sunset (Pilson and Pilson 1967); secondly, it would appear that the area which is searched by the tsetse during its feeding activity is extremely restricted, to judge by the very low dispersal rate of flies in their natural habitat (about 200 yards per week, see Glasgow 1963). In view of this, a low probability of host encounter is not surprising, even for a tsetse population which inhabits regions that support a heavy density of suitable hosts.

It can be seen from Fig. 1 that the replacement thresholds are situated on relatively steep slopes of the curves, suggesting that in stable populations of tsetse fly any change in the distribution or abundance of game, in so far as it would be coupled with corresponding changes in the value of P, should be reflected in associated shifts in population density, allowing for the time lag of reproduction. At first sight this prediction would appear to be contrary to common experience. Shooting operations usually have to go on for quite a long time before any effect can be detected on the tsetse population. It is likely that this apparent anomaly is associated, in part, with the social nature of many game animals, and particularly of the favoured host of the tsetse fly, the warthog. What is relevant in the present context is the chance that a tsetse has of encountering an opportunity to feed, whether this is provided by a single warthog or by a group of ten warthogs. To eliminate one or two warthogs of such a group does not affect the tsetse fly if it can still get a meal from others. One does not reduce host encounter probability until one has eliminated the group, and if the effect of shooting is to break up large groups into smaller groups, the chances are that during early stages of a shooting operation, there may actually be an increase in the probability of host encounter.

The main feature of interest in the relationship between encounter probability and life expectation is one which is unlikely to be affected by any of the inaccuracies which may have been introduced by over-simplification of the problem, namely the deep inflection of the

curve over its lower range. The form of the curve here implies that the expectation of life will be raised very little as the host encounter probability is raised from zero to a value of 0.5 in the hot season and 0.2 in the cold season. It shows, in other words, that not only should it be unnecessary to exterminate game, but that successful tsetse control should not be incompatible with a reasonable density of suitable hosts, to say nothing of game generally. This concept receives direct support from the Shinyanga game experiment (Potts and Jackson 1952). Here the intention was to exterminate all large animals, from impala upwards, but to leave smaller animals, mainly warthog, bushpig and smaller antelope. In the event, it proved impossible to curb the "hunting instincts of the African shooters", so that a considerable number of smaller animals were in fact killed; but it was estimated that a population of such animals totalling between 10 and 20% of the total population of game originally present, and including the animal which has since been recognised as the favoured host of the tsetse, remained at the end of the shooting campaign, yet the tsetse population had been totally eradicated.

The indications then, both from the mathematical model and from practical experience, seem to be that it is by no means necessary to reduce encounter probability to zero in order to exterminate the tsetse fly; all that may be required is to bring it down to a certain specific level which, given the requisite information concerning host/fly relationships may be to some extent predictable. What must be emphasised, however, is that to achieve the requisite reduction in encounter probability, it may be necessary to destroy a very large proportion of the game, if game destruction is carried out, as it usually has been and as it was at Shinyanga, in a completely random manner without regard for known facts about the biology of the tsetse and game. For instance, it might be necessary to eliminate 90% of the warthog population in order to reduce the chances of encounter by quite a small amount, because of the tendency for large social units to be fragmented; alternatively, a lot of impala might be exterminated without producing any detectable effect on the probability of encounter of *suitable* hosts, since impala is not a suitable host and is very rarely fed on by tsetse. But if game operations could be carried out with due regard to the necessity for reducing specifically the number of suitable encounters, rather than just the number of animals; and if this could be done on the basis of a thorough knowledge of the feeding pattern and feeding behaviour of tsetse flies in the area concerned, and of the biology of the main host animals, then it would seem not impossible that extermination of the tsetse might be achieved at relatively small cost to the wild life resource. In fact, one might go so far as to speak of the control of tsetse, not by game destruction, but by game cropping.

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APPENDIX 1

Calculations for the hot season are based on the following assumptions:
  (*a*) the mean hunger cycle is three days;
  (*b*) the mean duration of life without food is four days following a blood meal and
         three days following emergence from the puparium;
  (*c*) the feeding span is two days.
  The relation between daily probability of host encounter and longevity is then calculated
as follows.
  With a daily encounter probability of 0.00, the probability of finding a host during the
feeding span is also 0.00, so that emerging flies will live until they have exhausted their food
reserves, that is for three days.
  With a daily encounter probability of 0.10, 10 out of 100 flies will feed on the first day
of the feeding span, and of the 90 that do not feed on the first day, 9 will feed on the second.
The total of flies which succeed in getting a first meal is therefore 19, the corresponding
probability of host encounter during the feeding span 0.19. Similarly, for daily encounter
probabilities of 0.20, 0.30, 0.40 etc., the feeding span probabilities will be 0.36, 0.51, 0.64 etc.
  With an encounter probability for the feeding span of 0.19, all flies will live through the

first (teneral) hunger cycle; 19 out of 100 flies will succeed in entering upon the second hunger cycle, and of these, 3.61 (19 x 0.19) will enter the 3rd, 0.69 (3.61 x 0.19) the fourth, and so on. The average number of hunger cycles lived is therefore (100 x 1) + (19 x 2) + (3.6 x 3) + (0.69 x 4) ... /100 + 19 + 3.6 + 0.69 ..., which is 1.23.

For the sake of simplicity it is assumed that the flies which feed during a particular feeding span do so on average half way through the feeding span. The sequence of hunger cycles will then be as follows:

Flies emerge on Day 0, and those which fail to feed die on the third day; those that feed do so on Day 2 and live for four days, until Day 6. The feeding span of the second hunger cycle extends from Day 4 to Day 6; on average, flies feed on Day 5 and live for four days till Day 9. Thus the 1-hunger cycle flies live for three days, the 2-hunger cycles flies for six and the 3-hunger cycle flies for nine days. The successive hunger cycles are therefore uniformly of three days' duration, so that if an average of 1.23 hunger cycles are lived through, the average duration of life is 1.23 x 3 = 3.69 days.

For the cold season, calculations are based on a hunger cycle of six days, a maximum duration of life without food following a blood meal of eight days (following emergence, of six days), and a feeding span of four days.