A Prospect of Tsetse Flies

An Inaugural Lecture

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An Inaugural Lecture
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by

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I HAVE felt some hesitation in choosing for my topic a problem as amorphous and unwieldy as that of tsetse fly control, especially since my own work has been very much on the fringe of this area, and on the few occasions when I have been at all closely involved with control operations it has been with disastrous results. I certainly cannot claim to be anything of an expert on tsetse control, and I must find my justification for discussing it, not in any special qualification of mine, but in the subject's own importance in the particular context of Rhodesia, and of Africa, today. Beyond this I have consoled myself with the thought that one doesn't, so far as I can judge, have to be an expert in order to pontificate on this particular issue, since everybody does it who lives in Africa.

A few qualifications will, however, be necessary in order to circumscribe the area of discussion. In the first place I must emphasise that the tsetse fly which I shall deal with is specifically *Glossina morsitans* Westwood, the savannah species common in Rhodesia. This is the species with which I have lived for the last 17 years and the only one which I am remotely qualified to talk of. And even this, perhaps, is not enough, because *Glossina morsitans* is an ambiguous insect. It has been looked at so long and so hard that it seems to be blurring a little at the edges, and what one discusses may no longer qualify fully as objective reality—each man, more or less, his own tsetse fly and for now, mine.

It is necessary to qualify, too, in another direction; because although this discussion will centre on the control of tsetse flies, I propose to speak only of certain methods of control, those which I shall call "biological," in the sense that they are aimed at the insect's biology. I shall say nothing of the possibility, for instance, of control by release of sterile males; nor do I propose to deal with insecticides, though I am sensible of the important part that insecticides have played, and will continue to play, in local situations and as a means of quick alleviation of a critical situation. But I do not believe that methods which are divorced from, or indifferent in relation to, the larger problem of land utilisation can ever make an impact on the tsetse problem commensurate with the scale of that problem. Africa has seen too many dismal examples of the divorce between tsetse reclamation and land utilisation; large tracts of country in East Africa, for instance, completely devoid of vegetation, bare of trees and tsetse flies and ready for the plough, but with no one to plough. Ultimate success cannot, I think, be achieved on a really large scale unless the eradication of tsetse is seen as part and parcel of the utilisation of the land, and it is through a biological approach to the problem that this can best be done.

An approach of this kind would clearly have to be based on a thorough knowledge of the biology of the tsetse fly, and this is available to us, for the history of tsetse research is a long one. It may be said to date from 1903, with the production of Austen's beautiful "Monograph of the Tsetse Flies," which was published by order of the British Museum.[1] This book was brought up to date in 1911, on the grounds that "a practical and detailed knowledge of tsetse flies is essential for the material progress of large parts of Africa," words that are as true today as they were 50 years ago. A great deal of effort has gone to the gathering of detailed knowledge since then, and Swynnerton's book on the tsetse flies of East Africa[2] summarises the progress made during the first 25 years. This great volume was published in 1936 and came to be regarded by the tsetse fraternity as the bible of their cult. It was followed 20 years later by Professor Patrick A. Buxton's authoritative account of the natural history of tsetse flies,[3] often flippantly referred to as the gospel according to St. Patrick. By this time heavy books had gone a little out of fashion and the latest addition, Glasgow's "The distribution and abundance of tsetse flies," published in 1962,[4] is mercifully slim. To these general works must be added a number of books on special aspects of the subject and a multitude of scientific papers. Buxton's biography makes reference to no less than 700 articles, and since its publication I would estimate that the scientific literature on tsetse has grown at the rate of not less than 30 papers a year, bringing the score well into the three-figure range. Certainly the early injunction to build up knowledge about the tsetse fly has been well heeded, and I am confident that no other insect can rival *Glossina* in point of documentation.

There is, however, another and a bleaker side to this coin, for by very virtue of the antiquity of his subject the tsetse research worker is in the unenviable position of being able to compare the tsetse situation then and now. Due allowance has to be made for improvements in cartographic and survey techniques, but the picture that emerges is a gloomy one. There do appear to have been some changes in the distribution of the tsetse during the last half century, but there are few which can be unequivocally ascribed to the efforts of man. Despite the great quantity of information on the biology of the tsetse fly which has been gathered since the turn of the century, with the specific aim of facilitating its control, the insect seems to be holding its own pretty well. In saying this I intend no disparagement of the efforts of the Tsetse Control Departments in various parts of Africa; without them the situation might well have been very much worse. But the fact remains that successes in the field of tsetse reclamation have been essentially local. There has been an alleviation of epidemic conditions in this area, cattle have been introduced into that; but there has been no real impact on a really large scale; there has been no instance where a tsetse belt has been pushed back deeply on a wide front. What seems to have happened is that while we have accumulated a great deal of knowledge about the tsetse, we have not attained to an understanding of its biology sufficient to form the basis of effective control, and it will be a part of my purpose to enquire into the nature of this failure.

The first thought that strikes one, faced with this depressing discrepancy between research effort and tangible reclamation success, is that the field of research may not have been such as to attract the top calibre of scientist. Perhaps it is not that the problem has been especially intractable, but that investigation has lacked in quality. It has been something of a relief to discover that this uncomfortable possibility can be dismissed out of hand, in the general sense if not in the particular case. We can muster, I think, as many great names as any corner of the zoological field. To instance only a few, there was Professor P. A. Buxton of the London School of Tropical Medicine, justly famous for his early experimental work on the tsetse and for his careful interpretations of its biology. There was Dr. C. H. N. Jackson of the Central Tsetse Research Laboratories in Tanganyika, whose early death from cancer prevented the full expression of his great ability, but whose reputation rests securely on the outstanding work that he did on the population dynamics of the tsetse fly. And there is Rhodesia's Dr. R. W. Jack, whose work on the physiology and behaviour of the tsetse, published in 1939,[5] was far ahead of the time in concept and represents an incredible achievement for a man with the varied duties of a Senior Entomologist in a Government Department of Agriculture. With such names as these on the roll, the thought that research output has lacked quality cannot be seriously entertained.

If the fault lies not in ourselves, then perhaps our lack of success might be attributable to some special recalcitrance on the part of the tsetse fly, as compared with other insect pests, like the locust or the mosquito, which appear to be susceptible to effective control on the basis of a much slighter knowledge of biology. I would suggest that the tsetse does in fact seem to be so set apart from other pests in respect of a feature which would be of particular importance in relation to biological control—in the degree, namely, to which it appears to have achieved independence of its environment.

The tsetse fly's peculiar mode of reproduction provides a good example of what I mean by independence of environment. It is described by the rather unlovely phrase "adenotrophic viviparity," which signifies that the female tsetse fly does not lay eggs, as do the females of most other insects, but retains its fertilised egg within its own reproductive tract. Here the egg undergoes development to produce a succession of larval instars. The process involves a number of exquisite morphological and physiological specialisations, of which perhaps the most spectacular is the development, during early phases of pregnancy, of the so-called choriothete. The structure and function of this organ has been described by Dr. C. H. N. Jackson,[6, 7] who first discovered it. It consists of a tiny cushion of glandular cells, backed by a complex of muscles, and it is situated on the floor of the uterus near its anterior end. When the egg descends from the ovary its shell, or chorion, becomes attached to the cushion of cells, and at the completion of embryonic development the underlying muscle serves to peel off the shell, once it has been split by the minute "egg-tooth" of the first instar larva, and so to release the larva into the uterine cavity.

At this stage another specialisation of the reproductive tract comes into play to ensure the adequate nourishment of the young larva. From a small orifice in the roof of the uterus there pours a nutritive secretion, rich in protein and fat, which has been elaborated in special "milk"-glands of the pregnant female.[8] This secretion is sucked up by the larva and serves to sustain it during subsequent periods of development. As it takes in food the larva grows in size and moults to become a second instar larva, the choriothete again playing its part in the removal of the larval skin. With further growth a second moult occurs within the uterus and the pregnancy reaches full term with the production of a third instar larva. This is an animal of substantial size, weighing almost as much as its mother. It has the appearance of an ordinary white maggot, except that it is adorned by two intensely black and hard lobes at its posterior end, the intricate anatomy of which suggests that they may have played a part in intrauterine respiration.[9] This maggot is finally deposited by the female on the surface of the soil, into which it burrows to a depth of a few inches. Here it contracts to a barrel shape, and its soft larval skin immediately starts to darken and harden to form the puparium, within which a further protracted period of development takes place. Another moult occurs within the puparium, followed by extensive histogenetic reconstruction, in the course of which the larva is transformed from what is little more than a bag of nutritive secretion into a recognisable tsetse fly, tightly folded within the confines of the hard puparium. After this period of subterranean development, which varies from 20 to 100 days, depending on the temperature, the adult emerges. A special eversible sac, called the ptilinum, is inflated by hydrostatic pressure of the body fluids, thus exerting force on the anterior walls of the puparium, which ruptures along preformed lines of weakness. The fly now makes its way to the surface of the soil, expands its wings and is ready to embark upon the life of a tsetse fly as most people know it.

I have described the reproduction of the tsetse fly in some detail because it illustrates so well what I consider to be a general feature of tsetse biology, namely, the attainment of a high degree of independence of the environment. The peculiar mode of reproduction, based on far-reaching morphological and physiological specialisations, constitutes, in fact, an almost complete withdrawal of the developmental stages from the environment. The earliest larval instars have their own private environment in the mother's uterus and are thus shielded from the harshness of the outer world. Contact with the general environment cannot, in the nature of things, be indefinitely postponed, but when it does occur it represents at first no more than an exchange of shelter—that of the earth for that of the maternal uterus—with free-living existence limited to a brief moment of burrowing. The effectiveness of a few inches of soil as a buffer against environmental fluctuations in temperature and humidity, and as a protection against the attack of parasites and predators, cannot be doubted. And both are testified to by the relatively indifferent attitude of the pregnant female to the problem of larviposition. Soft soil and a shady place are all that are required,[10] and this is provided by a wide variety of overhanging objects such as fallen logs and rock ledges, or of cavities such as rot holes in trees or ant-bear holes in the ground. Soft soil is a prerequisite for successful burrowing of the larva, while shade is of importance because prolonged exposure of pupal sites to the direct rays of the sun could raise the temperature to levels which might be lethal to the developing insect. These basic requirements would be abundantly met in most natural environments, and the female is left free to choose a quite bewildering variety of sites for the deposition of its larva.

The reproduction of tsetse flies thus provides some striking examples of the attainment of a partial independence of the environment. But in relation to the adult stages, too, we find a series of delicate adaptations which, though hardly as spectacular, are none the less effective to this same end. A small animal like a tsetse fly, inhabiting an arid environment, as the tsetse fly does for the greater part of the year, will be under the continual environmental threat of desiccation. Because of its small size, the surface area through which water is lost will be large in relation to the reserves of water which must sustain that loss. If it is to achieve independence of the environment in the context of water balance, it must therefore be capable of exercising an extremely strict and delicate control over its water loss, and this the tsetse fly does.[11, 12] There are three main ways in which it may lose water: by transpiration through the cuticle; by diffusion from the respiratory system; and as a vehicle for the removal of nitrogenous waste products in the process of excretion. The loss by transpiration is minimised, in the tsetse as in most other insects, by the presence at the surface of the cuticle of a thin layer of wax, which makes it very impermeable to water. Losses from the respiratory system are controlled by spiracular valves which guard the entrances to the system. If the insect is well hydrated and the environmental humidity high, these valves are allowed to remain open, and water diffuses freely into the atmosphere from the moist surfaces of the tracheal system. But if the insect is in a state of dehydration, or if the air is dry, then the valves are kept partially closed so that the loss of water vapour through them is reduced. A similar situation exists in relation to excretory losses. For some time after it has fed, the insect has an adequate supply of water and there is a copious excretion of semi-liquid excrement. But if the water reserves are low, following exposure to dry air, then water is actively resorbed from faecal material, which is voided as an almost dry pellet. These control systems operate to such effect that the water content of tsetse flies in their natural environment appears to be completely independent of the humidity of that environment. At a given stage in the hunger cycle, water content is the same at the height of the dry season, when the relative humidity may be in the region of 30% or less, as it is in the middle of the rains, when the atmosphere may be nearly saturated with water vapour.[13] By virtue of these control systems, environmental humidity appears to have become a matter of complete indifference to the tsetse fly.

A second feature of the physical environment which would be of great importance to the tsetse fly is temperature, but here the scope for control is limited. The only way in which animals can effectively cool themselves is by the evaporation of water, as in sweating or panting. In view of the scant resources of water at the disposal of animals as small as the tsetse fly, this is a method which would have to be used with discretion. It has in fact been shown that in the tsetse fly evaporative cooling is not brought into play until temperatures approach quite close to the upper lethal limit of about 43°; only at this point do the spiracles open wide, and the rapid evaporation which then takes place from the respiratory surfaces serves to depress the body temperature by a degree or two and so to prevent a thermal death.[14] This should clearly be considered as in the nature of a crisis mechanism, to be brought into operation in moments of special danger, as for instance when the insect is feeding on an animal in the sun and so unavoidably exposed to direct insolation. For the most part the tsetse appears to rely for its thermal comfort on a wide tolerance to temperature extremes and on behaviour mechanisms which keep it out of the sun when the temperature is high. It can thus in no sense be said to have gained independence of temperature, but to do so, for an animal of such small dimensions, would be next thing to a physical impossibility.

The picture which I have tried to present is one of an insect that has gone a considerable way towards mastery of its environment; not just in the sense that any existing species of animal may be said to have mastered its environment in so far as it remains extant, but in the sense that the tsetse is in a position to display some measure of indifference to its environment. It has ceased, by virtue of various physiological specialisations, to be tied to a limited set of environmental conditions. It is not confined to regions of high or of low humidity; its developmental stages, unlike those of the mosquito or the locust or the blowfly, do not depend for their well-being on a particular set of circumstances—a pool of free water, an area of moist soil or a piece of decaying meat. As far as the physical factors are concerned, all it needs, basically, is a little shade so that its pupa and itself can escape the dangers of insolation. In saying this I have probably simplified the situation to the point of absurdity; have produced a caricature instead of a portrait. But caricatures often depict an aspect of the truth, and if this one does, then there are certain implications which should be examined. One might expect, for example, that if the tsetse has indeed achieved a partial independence of the physical features of its environment, then its behaviour in relation to such physical features might be characterised by a high degree of plasticity, in contrast to the often stereotyped behaviour patterns of other insects; this might, indeed, be a part of the reason for the extreme intractability of tsetse flies as objects of behavioural investigation. Under laboratory conditions tsetse flies simply do not behave. With most other insects reactions to temperature, humidity, light or smell can be profitably investigated under highly artificial conditions. If you put a mealworm beetle into a glass chamber which is humid on one side and dry on the other, the insect will react to the difference in humidity by moving into one half or the other of the chamber. If you put a tsetse fly into such a chamber it will stay where you put it. It is not interested in humidity nor in smell nor, very much, in temperature or light. It staunchly refuses to be duped into responding predictably to these simple physical stimuli, and the reason might be that it does not respond in a stereotyped fashion to such stimuli under natural conditions. Because it is so well buffered against physical features of the environment, it does not need to seek out a particular set of conditions and is therefore not provided with a set of stock responses, as are so many other insects. And such a peculiarity on the part of the tsetse fly might be of considerable relevance to the general problem of control. It could be here, for instance, in the plasticity, the opportunism, of tsetse behaviour that the answer lies to the failure of one of our traditional methods of tsetse control, the method of discriminative clearing.

The theory of discriminative clearing, in so far as it may be said to have a theory, is based on the concept of stereotyped behaviour. The idea of discriminative clearing arose out of the observation that tsetse populations appeared to be unevenly distributed in the general environment; that certain areas, which were called concentration areas, carried a much higher density of fly than others. These concentration areas could often be recognised on the basis of vegetational features, sometimes as a contact between two vegetation types, sometimes by the presence of a double-storeyed canopy, and so on. It was never clear exactly what the significance was of such areas to the tsetse fly, but the presence of tsetse in high density was assumed to be the expression of some innate behaviour pattern, an attraction for the tsetse of that particular concatenation of physical features. And it was argued that there must be a good reason for such a behaviour pattern, that it would be adaptive in relation to species survival, even though the reason was not manifest to the tsetse ecologist. The concentration areas were seen, in other words, as playing some special part in the economy of the tsetse population, and it was reasoned that if the physical features of the concentration area could be sufficiently altered by cutting down the trees, for instance, then the tsetse population would be eliminated.

I must emphasise that this account of the rationale of discriminative clearing is essentially apocryphal. I have not been able to find in the literature any definitive exposition of the theory of discriminative clearing. What I have related is no more than what I recall as being the general substance of discussions which took place among tsetse ecologists at the Central Tsetse Research Laboratories at about the time when the concept of discriminative clearing was born.

The idea behind discriminative clearing was, on the face of it, a good one, in an empirical sort of way, and it received tremendous support from a first and apparently successful operation at Abercorn in Northern Rhodesia.[15] On the basis of this initial success it was applied on a large scale in parts of East Africa, but with indifferent results. In some places there appeared to be a substantial reduction in population density following treatment, but in others the effect was negligible. It was at this point in time that we find a striking example of the innate stubbornness of scientists, so different from the face of impartial objectivity which they like to present to the world. We refused to recognise a failure when we saw one. We extended ourselves to find excuses for our lack of success in a dozen places, when what we should have done was to turn back to a re-examination of the first and only triumph at Abercorn. Had we done so we should not have lost sight of the fact that there had been an outbreak of rinderpest in the area just prior to the clearing operations, and that the consequent reduction in the density of game animals might have had something to do with the spectacular results achieved. But we decided to soldier on, even though evidence for the plasticity of tsetse in relation to vegetation became more formidable with every new situation that was investigated, even though the empirical basis of the method was eroding and a theoretical basis was all but lacking. In some areas the fly population would appear to be associated with the evergreen vegetation of major drainage lines; in others such vegetation was deserted in favour of an ecotone between savannah woodland and the open grassland of "mbuga"s or "vlei"s; in yet others the fly appeared to be associated with a sparse acacia woodland, with the trees widely scattered in rolling grasslands, and so on. There seemed to be progressively less in the way of a common denominator between the conditions favoured by the same species of fly in different regions of the country, certainly as far as vegetation was concerned. Or perhaps the common denominator was so common as to be useless for practical purposes, namely, shade.

Many will feel that I am adopting an unnecessarily extreme position in regard to discriminative clearing; that the method, though it may not be perfect, is yet of some use. Perhaps it is so, but I have had the misfortune to see some spectacular and very expensive failures, and for this reason I have raised my voice against discriminative clearing in private and public discussion for the last 10 years. Not that I have persuaded anyone to my point of view. On every occasion, I think, there has been someone who has countered my argument by relating that, although the results have not been reported in the scientific literature, yet at such and such a place a discriminative clearing scheme resulted in the complete eradication of the tsetse. I can only answer with the gentle equivocation of Horatio. "So have I heard, and do in part believe it."

The last nail has been driven into the coffin of discriminative clearing, I think, by the recent work of the Pilsons, here in Rhodesia.[16] These authors have shown that the apparent concentration of tsetse populations in specific parts of the general environment, on which the concept of discriminative clearing was based, may represent little more than an artefact of sampling. That it is not the whole population which is so concentrated, but only a small fraction of it, comprising males in a particular stage of the hunger cycle, when they happen to be particularly susceptible to sampling by traditional techniques. This discovery completely destroys the empirical basis of a control method which has no theoretical basis and which doesn't work. I will not proceed further with the post-mortem, except to pick up the thread of my earlier discussion concerning the relation between the fly and its physical environment. For it seems that in the failure of discriminative clearing we may simply be looking at another aspect of the same reality. In directing our attack against the physical environment, as we do in discriminative clearing, we are attacking the fly at the point where it is strongest. It has achieved a marked degree of independence of physical aspects of the environment, and it therefore remains unaffected by such alterations to the environment as we can encompass by means of discriminative clearing. We need to go to the end of this road to achieve unqualified success, to sheer clearing, whose effectiveness in the eradication of tsetse flies is well documented. Only at this extreme do we deprive the insect completely of its requirement for shade and so cause exposure of all stages of the life cycle to lethal levels of direct insolation. I would not like it to be thought that in saying this I am advocating wholesale clearing of vegetation as a control measure, because I am not. All I am trying to say is that unless one does this, one may do nothing.

If we can accept, for the sake of argument at least, that discriminative clearing is a failure, to what alternative do we turn? It should obviously be one where the attack would centre on what could be considered as a vulnerable part of the life history; a point at which the insect is closely dependent on environment, since it is through the environment that the attack must be made. And there can be little doubt that, viewed in this light, it is the relation between the tsetse fly and its host that constitutes the most vulnerable point. It is true that the feeding habit of the tsetse, its blood-sucking mode of life, involves as many striking morphological and physiological specialisations as any other function. One thinks particularly of the structure of the mouth-parts, to whose efficiency in piercing the epidermis of vertebrates most Rhodesians will testify, and whose modification for this purpose has involved a wide departure from the ground plan of insect mouthparts.[17] And there are other less apparent but no less fundamental specialisations. The salivary glands, for instance, whose secretion contains an anticoagulant that prevents clotting of the blood during its passage through the fine tracts of the alimentary system.[18] The midgut, where proteases, for the digestion of blood proteins, predominate over other types of enzyme.[19] The excretory system, which functions in the quantitative elimination of certain nitrogen-rich constituents of the blood meal.[20] And even the basic metabolic system, which shows certain peculiarities that can be seen as specific adaptations, at the biochemical level, to a diet rich in protein.[21]

Thus the habit of blood-sucking is reflected deeply in the structure and physiology of the tsetse fly, but the specialisations involved only serve to emphasise the very close relation which exists between the insect and the corresponding element of its biotic environment, the vertebrate host. Unlike the reproductive specialisations which I described earlier, there is here no question of a withdrawal from the environment nor of achieving any partial independence of it. Here the insect is closely linked with the outer world, and it is not surprising that the behaviour of tsetse flies in relation to their host is characterised by a lesser degree of plasticity than is their behaviour in relation, for instance, to larviposition. Here is the one example of a rigid behaviour pattern which can be elicited without fail under highly artificial conditions. For you can induce a hungry tsetse to probe quite unsuitable surfaces in quest for blood—a piece of paper, for instance, or a glass slide—provided the temperature of the surface is raised to about 39°; and, at a different level of behavioural complexity, the beautiful work of Weitz and his collaborators[22-25] on the identification of tsetse blood meals has demonstrated the existence of quite well-defined, almost stereotyped patterns of feeding. In most areas, for instance, between 60% and 95% of the meals of *Glossina morsitans* are taken from warthogs, with elephant, kudu, bushbuck and buffalo as common second favourites.* Species such as impala or zebra, despite the fact that they often abound in tsetse habitats, are very rarely fed on by the insects. Needless to say, in dealing with a species as versatile as the tsetse, evidence of opportunism is not altogether lacking. In certain

* The scientific names of game animals mentioned in the text are given in Appendix I.

areas and at certain times of the year animals other than the favoured few may bear the brunt of the attack from tsetse flies, but this is the exception, not the rule.

The idea that we are dealing here with a vulnerable point in the life cycle of the tsetse receives support from a consideration of the physiological state of flies in their natural habitat. This shows that a high proportion of flies which come to bait animals to feed are in the last stages of inanition, their food reserves at a level which would sustain life for very little longer.[26] Had they not encountered the bait animal at that particular time they would quite likely have died of starvation; so that starvation, through failure to make contact with a suitable host, must be a common cause of death in natural populations and perhaps a primary factor in the population dynamics of this insect.[27]

Here, then, we have a point in the life history where the tsetse is relatively rigidly linked with the environment and which would therefore constitute an area of particular vulnerability. I need hardly mention that this point is not a new one nor did it escape the notice of early tsetse ecologists, though it has, perhaps, never before been quite so tortuously argued. It formed the basis of a control method which is still with us, namely, the method of game destruction or game eradication, and it is with this subject that I want to concern myself in what time remains to me. I realise that since it is a method which involves the killing of animals it may not be an altogether suitable topic for one who professes zoology. But it is too important in relation to the problem of tsetse control to be ignored, and I hope I may be forgiven for introducing it.

The first thing that needs to be said about game destruction as a method of tsetse control is that it is based on sound theoretical foundations. The tsetse has no other source of food or of drink than the blood of vertebrates, and it follows that destruction of the vertebrate fauna must inevitably lead to eradication of the tsetse fly. That it does, in fact, do just this has been unequivocally established by a carefully conducted field trial carried out in Tanganyika as long ago as 1945;[28] and it has been confirmed, less rigorously, in the experience of tsetse reclamation departments in many different parts of Africa. Here, then, is a method of control which appears to be directed against a vulnerable part of the tsetse's life cycle, which has an impeccable theoretical basis and which can be made to work. As such it is not one which should be lightly dismissed.

Having said this, one must also admit to its one fatal flaw. It involves the wholesale destruction of mammalian fauna which, setting aside the breathtaking inelegance, is intensely repugnant in the prevailing conservationist or preservationist climate of Africa. The few control departments that still have the temerity to practise this method of control tend to be held in scorn by an outraged general public. Unfortunately the situation has by now become so charged with hysterical overtones that objective appraisal is a matter of great difficulty. The emotive use of language is practised with greater abandon in this than in any other field of science, and phrases like "destruction of our wild life heritage," or "senseless slaughter" are not uncommon, even in the scientific literature. It is not that I would advocate a withdrawal from reality behind a cloak of words. If we have to kill an animal let us by all means say so, but I do not see that there is much to be legitimately gained by calling it slaughter. And since I am bound to speak in favour of the method, by a conviction that control through the vertebrate host holds out the greatest hope for a solution to the whole tsetse problem, I hope I may be forgiven for digressing briefly on an aspect of the situation which is perhaps philosophical rather than zoological.

In order to eradicate tsetse flies by the method of game destruction a very great number of vertebrates have to be killed, and opponents of the method like to produce lists of figures showing the numbers of different species of game killed in any one year in any one region. These lists usually add up to an impressive total but, like most large numbers, it has little meaning unless it is compared with other numbers.

For instance, the average number of animals shot per year during tsetse control operations in Rhodesia from 1957 to 1960, when game destruction was widely practised as a control measure, was about 18,000. This is a formidable figure, but it must be set in the general context of killing of which it is one element. Thus in Rhodesia the number of animals shot by sports hunters in the Zambesi valley alone averages 3,600 a year; the number of animals which have to be destroyed for crop protection, etc., may be as high as 17,000 in one year; animals killed under land holder's licences total approximately 10,000 a year, and the number allowed for commercial utilisation under game cropping permits 12,000.[20] I hope it will not be considered frivolous if I mention, too, that some 350,000 head of cattle are killed in Rhodesia every year, and if we add pigs and sheep and poultry the number soars into the millions. In this total pattern of death the number of animals killed in tsetse control operations emerges as a relatively minor element; not that this in itself can justify the killing, but it does suggest that the fierce disapprobation in which tsetse control personnel is held, as against the sports hunter or the game rancher, may be a little unrealistic.

A wild life conservationist would doubtless argue that to introduce considerations of domestic stock is a flagrant irrelevance, since a kudu is obviously a much better animal than a steer. The criteria upon which such a judgment is made might not be acceptable to everyone, but there is admittedly a valid distinction to be drawn between wild life and domestic stock where species are concerned that stand in danger of extinction. This, however, cannot be claimed for the species with which we need to concern ourselves in the context of tsetse control, and my position is, therefore, that if it is necessary to control tsetse flies and if, in order to do so, we need to kill a large number of game animals, then this is a fact which we must learn to live with, as we have learnt to live with the killing of animals for food or for any other necessary reason. I appreciate that without a definition of the word "necessary" this begs the ethical question, but I have trespassed long enough on preserves that are foreign to zoology.

I submit, then, that the control of tsetse through their biology can most hopefully be directed at the area of contact between the tsetse and its host; and I accept that, as generally practised, the method of game destruction is anathema to an overwhelmingly large sector of public opinion. What remains to consider is whether there is any likelihood of achieving a diminution of the repugnant aspects of the control method without affecting its essential soundness. And I believe that there are good grounds for supposing that this can be done.

It is possible to investigate the general relation between the tsetse and its host by means of a simple mathematical model, based on known facts of tsetse biology and on the well-founded assumption that starvation is the most important natural mortality factor. Such a model shows quite clearly that eradication of tsetse flies is not dependent on the complete destruction of vertebrate fauna;[30] shows, indeed, that successful control should be capable of being achieved at a comparatively small cost to the vertebrate fauna. This conclusion receives empirical support from the game destruction experiment to which reference has already been made, for in that experiment only the larger animals were eliminated; species of the size of impala and below were not supposed to be shot. In the event it proved impossible to curb the natural hunting instincts of the shooters, so that a substantial number of smaller animals was, in fact, killed. But it was estimated that the proportion that remained constituted about 30% of the total number of animals originally present, and included among them was the warthog, subsequently shown to constitute the favoured host animal in that area. Yet the tsetse fly was completely eradicated.

There appear, then, to be both theoretical and practical grounds for thinking that the method of game destruction is one which may be capable of considerable refinement. And one basis for such refinement has already been provided by the discovery that certain species of game, notably the warthog, constitute the main source of food of *Glossina morsitans*. This was demonstrated nearly 15 years ago, but some form of intellectual paralysis has made us content to admire this discovery without making any attempt to follow up its implications, and these are enormous. In the first place, it raises the question whether tsetse flies can be controlled by destruction of just the favoured species. Judging by results obtained here in Rhodesia, the answer seems to be yes;[31] one can only wonder why it should have taken so long to perform the experiment and why it has not yet been performed in other parts of Africa.

But there are other implications of Weitz's work which should have been followed up. Granted that there are certain species of game which are regularly fed on by tsetse flies and others which are never touched, what is it that makes an animal a favoured host? And, conversely, why is it that tsetse flies are apparently prepared to die of starvation rather than take a meal off an impala, to judge by the fact that flies at the point of death can be captured within sight of a herd of impala. It does not appear to reflect any special unpalatability of the blood or the skin of impala, since flies will readily probe impala skin and can be maintained as readily on impala blood as on any other.[32] The reasons are undoubtedly manifold and complex; effective defensive mechanisms of the host may, in the course of evolution, have induced a negative response to certain species of game on the part of the tsetse; to be a favoured host an animal may have to stand in some special relation to diurnal rhythms of the tsetse, to be especially available at times of peak feeding activity soon after dawn or just before sunset: the animal may have to be in a certain situation, and perhaps at a low level of alertness, at the right time, and so on. What is involved here is the intimate relation between the tsetse and its host, and what we need to know is the detailed pattern of behaviour of one in relation to the other. This is a subject about which we have at present virtually no information; nor, except in Rhodesia during the last year or so, has there been any attempt to obtain such information. Yet this aspect is rich in promise for the substantial refinement of technique, in so far as it raises the possibility that eradication of the host may not be an essential prerequisite of effective control; that the link between the tsetse and its host may be capable of being broken by management, rather than by destruction, of the host; by an alteration of the environment such that the host fails to present itself to the tsetse at the right time or in the right place. It could even be this that we in fact blindly do when we have some measure of success with discriminative clearing.

There is a third possibility of refinement that should be considered, again one which would have to be based on a thorough knowledge of host biology. What is important in relation to the population dynamics of the tsetse fly is the chance that the average fly has of encountering an opportunity to feed before it has exhausted its food reserves. Such an opportunity may be provided equally by a group of 10 warthogs or by a single warthog. To reduce the probability of host encounter it is pointless to eliminate one warthog out of a group of 10, since this may leave the situation unaltered. Indeed, if the effect of shooting is to break up large social units into smaller ones, then the result of shooting may well be to increase rather than to decrease the probability of host encounter. One might eliminate 90% of the warthog in an area without achieving any reduction whatever in the chance that the average tsetse has of encountering a warthog. In other words, where destruction of game has to be carried out, it must be done, not at random, but with due regard for species biology and in such a way as to reduce, not just the number of animals, but specifically the probability of host encounter.

Taking these three points alone—the possibility that only certain species would need to be controlled, the possibility of facilitating a break in the link between host and tsetse by some form of manipulation of the environment, and the possibility that a thorough knowledge of the biology and social structure of the host animals might enable us to direct our attention to the reduction of host encounter rather than just the elimination of animals—taking just these three, it is evident that the technique of game destruction may in fact be capable of very substantial refinement, refinement to the point, conceivably, where effective control measures would become acceptable to even the most uncompromising conservationist; where, in fact, one might speak of the control of tsetse not by eradication of game, but by management of game. And it is only on such a basis, I think, that one could hope to make an impact on the tsetse problem which would show on the map of Africa.

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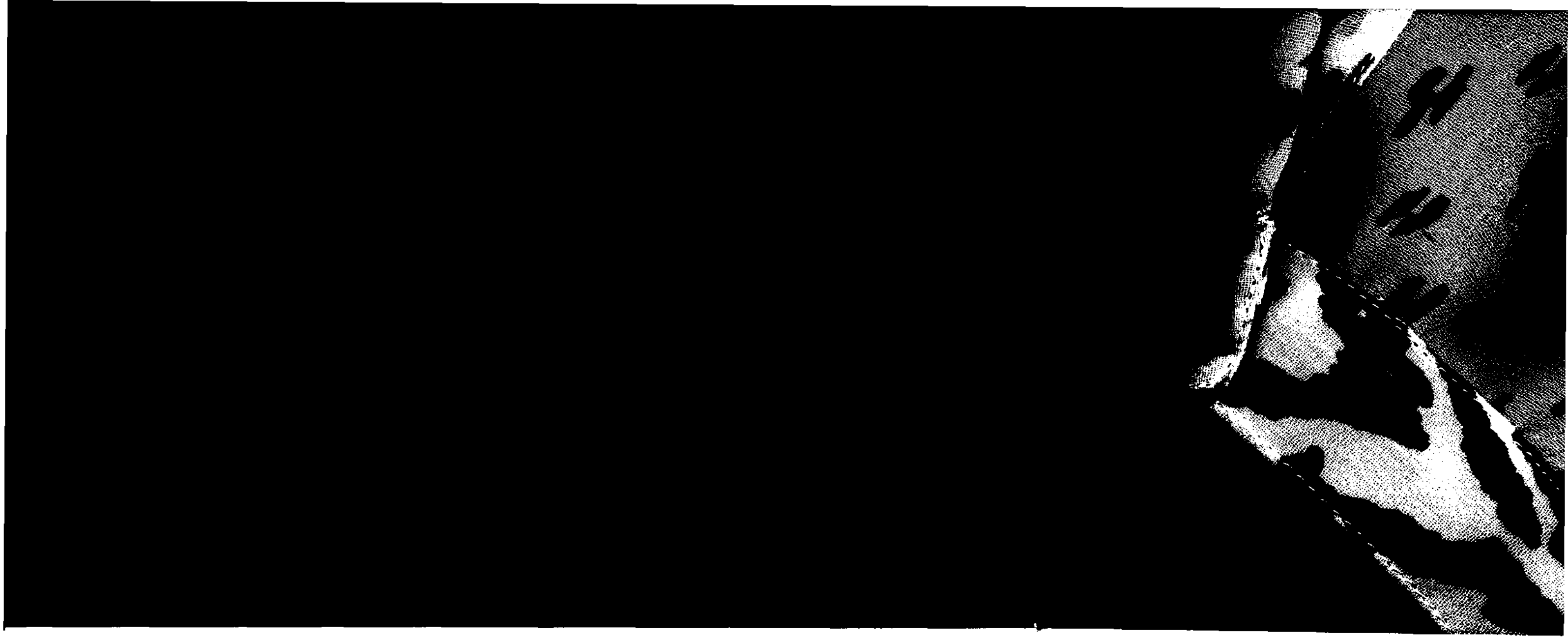

APPENDIX

Buffalo: *Syncerus caffer* Sparrman.

Bushbuck: *Tragelaphus scriptus* Pallas.

Elephant: *Loxodonta africana* Blumenbach.

Impala: *Aepyceros melampus* Lichenstein.

Kudu: *Strepsiceros strepsiceros* Pallas.

Warthog: *Phacochoerus aethiopicus* Pallas.

Zebra: *Equus Burchelli* Gray.