study
workshop
on

TSETSE ECOLOGY AND BEHAVIOUR

28 September
2, October 1976

SUMMARY OF PROCEEDINGS AND DISCUSSIONS

INTERNATIONAL CENTRE OF INSECT
PHYSIOLOGY AND ECOLOGY (ICIPE) P.O. Box 30772 NAIROBI KENYA

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Preface

The International Centre of Insect Physiology and Ecology (ICIPE) has made it a central plank of its policy on scientific dialogue to convene from time to time a small Study Workshop to examine critically selected areas of pest research which are of pivotal importance in the attainment of the research goals of the ICIPE. Each of these Study Workshops consists of 25 to 30 working specialists in their disciplines, some of whom work in research laboratories while others are in business of appying new research results in the field. We believe that the interplay between these two facets of pest research is important, particularly in tropical areas where this has not been a general pratice.

Tsetse flies, as vectors of human and animal trypanosomias in Africa, are a major concern throughout much of tropical Africa — and has been so for thousands of years in Africa. In June 1973, the ICIPE, in collaboration with the Rockefeller Foundation, convened a Study Workshop at Bellagio, Italy, on "Parasite/Vector Relationships with Particular Reference to the Tsetse Fly." The present workshop, held in September 1976 in Nairobi, is concerned with "Tsetse Ecology and Behaviour ."

Much of the circumstance surrounding the success of tsetse flies as vectors of the dreaded trypanosomiasis is to be found in their behaviour and ecology. In spite of their very low reproductive potential, and their often observed fact of relatively low population levels in the field, yet trypanosomiasis continues to be a threat to much of Africa. Their highly plastic host-selection behaviour, their wide-ranging ability to adapt to new ecological conditions, theirsemi-social behaviour patterns, and many other aspects of tsetse life, were reviewed and discussed afresh in this Nairobi workshop.

An outline of the outcome of the workshop deliberations is now made available to a wider public. We sincerely hope you will share a sense of the pregnant environment in which this meeting of the minds took place.

THOMAS R. ODHIAMBO.

ICIPE RESEARCH CENTRE,
NAIROBI
30TH APRIL 1977

THE TSETSE STUDY WORKSHOP PLANNING COMMITTEE

Prof. Thomas R. Odhiambo	—	Chairman
Dr. L. H. Otieno	—	Workshop Co-ordinator
Dr. M. F. B. Chaudhury		
Dr. J. van Etten		
Mr. J. M. Ojal		
Mr. H. Awori	—	Recorder

Workshop Rapporteur	:	Professor E. Bursell
Assistant Rapporteurs	:	Dr. L. C. Madubunyi Dr. M. F. B. Chaudhury
Venue	:	ICIPE Library, Northern Star Building, Chiromo Campus, Nairobi Kenya
Dates	:	28th September, 1976 to 2nd October, 1976

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SCHEDULE OF EVENTS

Tuesday, 28th September 1976

MORNING

Registration	ICIPE, at The Northern Star Building

AFTERNOON

Opening Address	Dr. John J. McKelvey, Jr. (Chairman of the Study Workshop)

EVENING

Reception	Mayfair Hotel, Westlands, Nairobi

Wednesday, 29th September, 1976

MORNING

TSETSE ECOLOGY

The current status of our knowledge of tsetse ecology	Dr. A. M. Jordan
The ecology of *Glossina palpalis palpalis* is Lower Zaire	Dr. P. van Wettere

AFTERNOON

TSETSE ECOLOGY

Sampling problems with tsetse flies	Dr. G. A. Vale
Ecological and epidemiological aspects of atypical tsetse populations	Dr. D. A. T. Baldry
Interactions between various components of zoonosis of African trypanosomiasis in infected foci	Dr. S. K. Moloo

AFTERNOON

TSTTSE ECOLOGY AND BEHAVIOUR IN RELATION TO NUTRITION

Monthly and seasonal fluctuations of suspected abortion rates in a natural population of *Glossina morsitans morsitans* Westwood in the Republic of Zambia (1972-1975)	Dr. S. N. Okiwelu
Role of food in tsetse population dynamics	Dr. L. C. Madubunyi
Maintenance of tsetse flies in the laboratory: Some practical considerations	Dr. E. D. Offori

EVENING

Tanga tsetse fly project	Dr. L. Williamson
Slide show on tsetse habitats in Botswana	Mr. R. Allsopp

Saturday, 2nd October, 1976

Evaluation of Workshop Proceedings

Thursday, 30th September, 1976

MORNING

TSETSE BEHAVIOUR

Why study tsetse behaviour in the laboratory?	Dr. J. Brady
Tsetse feeding and salivation behaviour	Dr. A. Youdeowei
Studies on resting habits and diurnal distribution of the housefly, *Musca domestica* L. as related to fly control	Dr. J. Keiding

AFTERNOON

TSETSE BEHAVIOUR

Recent studies on mating behaviour of *Glossina pallidipes* Austen	Mr. T. Jaenson
Energy reserves and activity in tsetse flies	Professor E. Bursell

Friday, 1st October, 1976

MORNING

TSETSE ECO-GENETICS AND PATHOGENS

Developments in tsetse genetics: Prospect and retrospect	Dr. W. Helle
Eperiences with isoenzyme studies on tsetse flies	Dr. L. P. S. van der Geest
Preliminary studies on the susceptibility of *Glossina morsitan* to some insect pathogens	Dr. L. P. S. van der Geest
Comparative studies on two semi-isolated populations of *Glossina pallidipes*	Dr. J. van Etten

OPENING ADDRESS

By Dr. John J. McKelvey, Jr (Chairman, Study Workshop)

How many times does one ask himself why all the fuss about tsetse? Can't we leave those insects alone? Let them help maintain the ecological balance that people — mostly those from far away lands — treasure about the parts of Africa these insects occupy. Let tsetse continue to put people forever to sleep by innoculating them with trypanosomes. albeit less than 10,000 cases of sleeping sickness crop up among people of Africa annually now, 1/when thousands of thousands of cases used to. Let them and their trypanosomes serve as a morbid defense against cancer and other debilitating diseases which might afflict the patient, if tsetse and trypanosomes, along with such other infectious agents, as the malaria parasite and the parasite that causes river blindness did not get to him first. Let tsetse keep cattle out of vast areas of Africa and force people to domesticate other beasts or to do without.

Not yet are tsetse flies so benign to us and to the animals we choose for our livestock that we can let them be. Not until they cease to be vectors of sleeping sickness in man and trypanosomiasis in cattle. Human nature dictates that we continue to command the talents and elicit the brilliance of men and women to find out what makes tsetse flies and trypanosomes tick; that we devise ways to control them which are not only ingenious against tsetse but which may be exemplary in the control of other pests as well. We must mount action programmes. We must build research institutes ICIPE, ILRAD, EATRO, NITR and the like. And we must sometimes even waste manpower, money and materials for the high risk and multiple risk experiments which may pay handsomely in the results to be achieved or which we may have to be prepared to say with satisfaction, even pride: it was a great experiment — but it didn't work.

Within the context of the past, present and future of the fly, and of the trypanosomes, cattle and man in Africa, this study workshop is convened. The business of the participants, each from the vantage point of his specialization, his institutional experience, his skills and his intellect is to conceptualize, to chart a course for future research into the reproductive behaviour, the ecogenetics, the vectorial capacity and the other aspects of tsetse, especially, as tsetse may help or hurt mankind.

Insofar as reproductive behaviour (pheromones), ecogenetics (biological engineering), vectorial capacity and similar characteristics of the fly bear upon methods for its control they ameliorate man's zeal to roll back the fly by one technique alone — insecticides. Even so, this zeal if directed to eradication can turn into a passion. Ormerod2/ might say that it had — in the Sahel. In a recent

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1/ Dr. Raadt. P *African Sleeping Sickness To-day* Trans. Royal. Soc. Med. and Myg. Vol. **70:** 114-116 1976.

2/ Ormerod, W. E. *Ecological Effect of Control of African Trypanosomiasis;* Science Vol. **191:** 815-821, Feb. 27, 1976.

issue of *Science* he imputed irresponsibility to man's efforts to eradicate tsetse from the Sahelian zone of Africa thus aggravating the seven-year drought and encouraging desertification by admitting to the area an overload of animals followed by people. But Ormerod may be paying an embarrassing compliment to man who, appearing to operate in the vanguard of the forces leading to the demise of lesser organism, is instead responding to natural forces he himself might not understand. And Ormerod may be underestimating nature's resiliency to cope with human as well as with insect and animal populations.

Aided by man, tsetse has retreated from strategic bases at the periphery of its range. This retreat has revealed the great potentialities for development that the Sahel possesses. Thought to be overpopulated with its present 25 million people, the Sahel may really be able to carry a far greater number of domesticated animals and people than it now sustains.

The Niger River could become a Nile in terms of water use for agriculture and for hydroelectric power, its flood plains far more intensively cultivated than now, to sorghum, rice, maize, relieving the pressures of agriculture from the hinterland where the normadic people on the Sahelian range might find it easy to modernize their present system. Pastoralists and agriculturalists, country and city dwellers might have to come to a better understanding of each others problems and in working out solutions of mutual benefit. UNDP, FAO, WHO, already are attempting to eradicate river blindness from the Volta river basin and schistosomiasis is under attack. Conflicts in international relations may arise, when the nine countries through which the Niger flows demand maximum output of its water. Would the African people trade these problems, trade these opportunities for Sahelian development for a return of tsetse and its trypanosomes to the places in the Sahel it once occupied?

Whatever the case with tsetse in the Sahel and in the Savanna zone to the south — ravaged or prepared for development the entomologist has played a supporting role as is proper in association with medical doctors, ecologists, agricultural production experts and others. This multidisciplinary approach will become important whether in institutional situations or in action and development programmes — we know, all too well, the overuse and the misuse of insecticides the world around during the past several decades. A. M. Jordan 3/ wrote recently "insecticides will undoubtedly be the main method of tsetse control for many years to come" and he is, of course, quite right. But that does not mean we have to rely indefinitely or exclusively on insecticide as defined narrowly and add fuel to the public image of the entomologist which is not as a professional with a comprehensive role to play but as a technician instead with flit gun or spray bomb polluting the atmosphere. And I will digress here to remind you that the entomologist has earned that image to some extent. The whole aerosol industry from insecticides to perfumes and shaving bombs owes its origin to the portable aerosol dispenser which used "Freon" 12 and which two entomologists developed when they sought a way of combating the insects which caused disease among overseas troops during World War II.4/

3/ Jordan, A.M.

4/ Sanders, Paul A. *Principles of Aerosol Technology* Page 11.

The "give them the works" concept applied to killing pests with empirically concocted non-selective insecticides must yield. It is yielding to programs aimed at fashioning insecticides in a logical way based on the insect's own body and behavioural responses to its environment, its food sources and its own internal chemistry and physiology. And the usage of traditional insecticides must give way to a clean-out-the-whole-arsenal-and-put-all-the-weapons-to-work concept which pest management and methods of integrated control embody although these two modern concepts are usually advertised in altruistic and euphemistic terms as alternative to persistent pesticide use.

Consonant with our objectives in the Rockefeller Foundation to combat hunger, to improve health, and to provide an adequate quality of life for people, we sought advice in 1970 from a group of prominent entomologists on ways and means of helping to lift the pesticide load on crops in the United States. The group recommended establishing four multidisciplinary, multi-university programs. One was to deal with biodegradable pesticides which will be synthesized to replace existing non-biodegradable persistent ones. Another with juvenile hormones as sources of selective insecticides. A third program focussed on pheromones for their potential impact on insect population dynamics and a fourth one concentrated on breeding plants resistant to insect attack. Vital to each of these programs was the enlargement of the crop of young biochemists, toxicologists, entomologists and related specialists who would be capable of broadening the base of knowledge which is essential to advancement in any one of these four strategic areas.

Six years and 4 million dollars later, the ideal non-polluting, biodegradable insecticide has not reached the market if indeed it has been synthesized but the whole character of the insecticide used against pests has changed. Juvenile hormones only in rare situations show some promise of practical use but hormone mimics and anti-juvenile hormones have been discovered. The grand experiment at a cost of $500,000 and more to shoo the pink ball worm off of cotton and out of the Coachilla valley of California by confusing the male moth with too much female perfume so he wouldn't know which way to turn to choose a mate and up the ballworm population didn't work, not from the standpoint of eradication, but other such experiments were successful and the chemical control of insect behaviour, conceptually is one of the most rapidly evolving fields of research in entomology today.And notwithstanding the remarkable success plant breeders have had in engineering plants to escape or resist insect attack the basic problem — similarity in food preferences among human beings and insects — remains.

Further to count our blessings, however, a large corps of entomologists stands ready to cope with insect control along new lines. Priorities in pesticide usage have been reordered. The public is well informed and the concept of what constitutes an insecticide has been vastly broadened.

The programs just described were aimed at direct host-pest relationships. But in the case of tsetse we're not dealing with just another insect in direct contact only with its host. We are dealing with the tsetse-trypanosome linkage and we must seek ideas that will lead to ameliorating the disease the trypanosomes cause. This means taking a hard look at the tsetse-trypanosome interface. In 1973, ICIPE convened a conference at Bellagio because in the words of Professor Odhiambo who chaired it: "We thought the biological relationships existing between the insect vector and the trypanosome parasite must be a vital one, and that it needed to be thoroughly examined if we were to have a critical understanding of a disease such as trypanomiasis" Just what that vector-trypanosome relationship is — parasitic ?, symbiotic ? — is not exactly clear to me, it needs clarification.

The conference advanced new concepts in tsetse-trypanosome biology. Three novel approaches stood out, namely, (a) to produce an antibody in the mammalian host which inhibits the activity of the anti-coagulant in the tsetse salivary secretion; (b) to study the genetics of those tsetse populations that are susceptible to trypanosome infection; (c) to discover a specific blocking agent for neuro-muscular or neurosecretory activity in tsetse flies. And, of course, most participants felt that deeper research should be carried out on these new possibilities with the intention of controlling tsetse flies through integrated programmes

To stretch our imagination as far as we dare we could explore the common grounds that may exist between animal and plant immunological systems. Some people doubted that any such grounds exist but in cross kingdom (plant/animal) distinguished we held in New York year ago with discussions scientists from each camp, rewarding information emerged with respect to Tissue culture, Cell biology, Vectorial capacity, Immunological systems, the Mechanisms of resistance to disease and symbiosis. For example, the participants singled out tissue culture as an area of research basic to an understanding of the disease-resistant process and as a means of unravelling the obligate parasite relationship in both plants and animals. Almost to prove the importance of that tenet, in the year following the conference two major advances occurred, the growth in tissue culture of *Plasmodium falciparum* at the Rockefeller Institute, and within the past few months the maintenance in tissue culture of *Trypanosoma brucei* with its ability to reinfect cattle after having been grown *in vitro*, at the newly created laboratory, ILRAD, in Nairobi.

They agreed on the importance of research in cell biology with reference to surface phenomena associated with antigenic variation on the animal side and receptor reactions of cells on the plant side.

In both plant and animal kingdom the role of insect vectors as processing agents for disease organisms was of prime concern. We know that the pathogen responsible for yellow fever, transmitted by the mosquito *Aedes aegypti* cannot multiply in all populations of that vector.

The immunological processes in plants constituted another area of comparison with those of higher animals despite basic differences in structure and physiology of plants *vs* animals. But we know that some plants can be immunized by a mild strain of the mycoplasma that cause Aster yellows which protect such plants against attack by certain more severe strains of mycoplasma which cause the disease.

Finally, they recognized the importance of symbiosis as the ultimate goal in man's interaction with the disease organisms, and with the pests and pathogens he strives to eradicate.

I have called to your attention three cases in which the Rockefeller Foundation has been involved in plant and animal protection: the search for alternatives to persistent pesticides, the study of insect-parasite interfaces, and the nature of resistence to disease whether the disease infects plants, animals or man-first to divulge where in our specific interests and concerns lie; second, to show how closely they tie to yours; and third, to tell you the process we undergo to try to ensure that the monies entrusted to us are well invested. These activities must not be viewed out of proportion to those of the entire network of universities, experimental stations, donor agencies -- multilateral and bilateral — and special institutes where research is in progress.

By constitution and by design, ICIPE affords exactly the kind of brainstorming opportunities just described. That's why we are here. Created as a discipline-oriented research institute it can and does bear down on the basic research essential to the subsequent development of action programs to combat insect pests of importance to man, agriculture, and his livestock. It's breadth of program — inclusive of sorghum shootfly, termites, ticks, and tsetse flies — must give the researcher the stimuli he needs from cross species, cross genera, cross family and even cross kingdom discussions. Links to its newly-created sister institution, ILRAD in Nairobi, to the community of African and of international scientists, must keep its workers alert to breakthroughs in scientific progress in entomology elsewhere.

Tsetse, the pest! weak enough to be bowing out of life in an evolutionary way — still has the power, possesses the strength to make people ponder over the appropriate relationships between insect and man. How much of a pest is tsetse? On whose say is it so? And what antics must we continue to perform in the name of economic entomology, and at the expense of our environment and of ourselves to kill it? Could it be that in the interaction between man and fly, tsetse would become precious enough to be held and admired as a jewel — a relic of bygone days? Or might it become one of our symbionts and thus fade into oblivion?

Tsetse flies — trypanosomes? Now wouldn't it be a shame if in one generation of human beings we would snap a system so mysterious, so delicate, so illogical, one that has bound together tsetse, trypanosomes, cattle, man, for millenia. Never fear. We won't, because we can't but we must try. We can and we will break one or two individual samples of the system better to understand, better to ponder it as a whole, but the system will survive us.

We could, in our long term view, take a lesson from Lord Asby who in *A Second Loot at Doom* suggests that "the formula for survival is not power; it is symbiosis".5/ He adds, "I don't believe we can devise fail-safe systems (in our case to get rid of tsetse and/or trypanosomes completely); what we have to devise are systems which will not foreclose options even if they do fail." In this study-workshop we are looking for those options — the most imaginative ones we can find — in order to reach a true understanding and to achieve a sensible management of the fly-trypanosome-man-cattle complex.

5/ Asby, Eric A Second Look at Doom, Encounter, XLVI (3) 16.24

SESSION ON TSETSE ECOLOGY

WEDNESDAY, 29TH SEPTEMBER, 1976

Dr. A. M. Jordan kicked off the scientific session of the Study Workshop with a presentation entitled "The Current Status of Our Knowledge of Tsetse Ecology."

He chronicled the development of, and major achievements in, tsetse ecology from the days of Swynnerton through the post-colonial era, stressing that both bilateral assistance programmes from non-African countries as well as multilateral assistance from international organisations have important roles to play in continued achievements in tsetse ecology. Using Buxton's "Natural History of Tsetse Flies" as his basis, Dr. Jordan reviewed selected topics in tsetse ecology pointing out the major developments since its publication nearly 30 years ago and highlighting gaps in our knowledge in those areas.

On "Sources of Food," Dr. Jordan observed that although we now know the types of hosts utilised by most species of *Glossina* and the variations that occur from one geographical area to another, we still do not understand either why some species of *Glossina* apparently prefer one species of host to another and how a tsetse fly recognises a host as unattractive.

On "Movement and Rest," he observed that while from laboratory we now have more information about individual fly movements, not all activities of adult tsetse flies in the field can be related to such external stimuli as temperature changes and olfactory or visual stimuli. He also observed that our preconceived ideas on tsetse population movements in relation to season and vegetation, which were based mainly on male flies attracted to man, need to be re-examined since more efficient sampling devices have now become available. He further stated that while we now know a lot more about the resting sites of *Glossina* species in general, critical studies must now be undertaken on individual species in each area where the selective use of insecticides is envisaged in order to avoid failure in our control programmes.

On "Tsetse and Climate," Dr. Jordan observed that there has been very little new data over the past 20-25 years.

On "Tsetse and Vegetation," he observed that although the basic association between tsetse and vegetation is well known and documented, recent examples of tsetse occurring in environments which previously had been considered either hostile or in which they had never or only rarely been recorded illustrates the adaptability of the genus.

On "Causes of Death," Dr. Jordan observed that although we have available a comprehensive list of known or suspected mortality agents we still do not known which of these are critical, how many tsetse flies are killed by any of them, and whether any of them could operate in a density-dependent manner.

On "Populations of Tsetse," he observed that qualitative data abound while quantitative data are very limited. This he atrributed to difficulties inherent in conventional sampling techniques, a situation which he hopes the new and ingeneous sampling devices recently developed by Dr. G. Vale in Rhodesia will ameliorate, since his findings are already making it necessary to re-examine many of our ideas about the structure and behaviour of tsetse populations.

Following a lively discussion of Dr. Jordan's paper, the participants came to a general agreement that future research in tsetse ecology should give priority to the following aspects:

1. Multidisciplinary investigations of the association between tsetse populations and those of their hosts
2. Characterization and quantification of mortality factors operating in tsetse populations
3. Quantitative analysis of tsetse populations with special attention being devoted to problems posed by species occurring in low densities.

Dr. P. van Wetteere gave a detailed description of his work on the "Ecology of *Glossina palpalis palpalis* in Lower Zaire" in an area characterised by a dense human population, a large number of goats, sheep and pigs, paucity of wildlife, and the presence of secondary fringing forests. This work was necessitated by the government's desire to curb human sleeping sickness, whose incidence had risen from a frequency of 0.02% in 1960 to 25% of the country's population in 1964. He reported an apparently direct relationship between temperature and number of adult tsetse flies captured by handnets and a dependence of apparent density on the presence of hosts in the fringing forests, other than man and his domestic livestock. He further reported that older females were attracted more to pigs than man. The activity level of the adult tsetse flies was apparently positively correlated with temperature and light intensity, the former and later being more important in females and males respectively. During the last two years of his investigations, Dr. van Wettere, using the mark-release recapture method, observed that *G.p. palpalis* travelled up to 5 km outside the fringing forest.

Dr. G. A. Vale, in discussing "Problems of Sampling Tsetse Flies", first highlighted the major areas of discontent with conventional methods so far employed in sampling tsetse populations, namely: their inability to yield samples large or sufficiently representative of the composition of wild tsetse populations, inability to relate confidently the level of catches at standard baits to level of tsetse densities, the desirability of having one sampling scheme effective for all tsetse species in all parts of Africa and which is applicable both to the catching-out method of population estimate and tsetse control respectively. He then outlined some intriguing patterns of tsetse behaviour, reflected in the variations in number and composition of catches of the tsetse when combinations of man, inanimate object, bait animals, and host odours are used, which gave impetus to his studies of improved tsetse sampling techniques in Rhodesia.

Concentrating on stationary baits only and total number of flies attracted to the vicinity of baits, Dr. Vale used a series of slides to show that electrocuting nets, which completely surrounded baits or which were placed in the densest part of the attracted swarm, caught nearly all (about 95%) of the tsetse flying into them. As such, he stated, electrocuting nets appear to be the best available means of assessing samples of tsetse initially flying towards baits in the field. These nets caught more females than any other existing tsetse catching method. Through their use, he was also able to demonstrate that the presence of man near stationary bait animals greatly reduced the attraction of *G. morsitans* and *G. pallidipes* to the bait animals. He attributes this to the repellent effect of human body odour. His work also demonstrated that a considerable proportion of long-range attraction of *G. morsitans* and *G. pallidipes* depends on olfactory stimulation since his catches increased proportionately with the quality of host odour released.

Dr. Vale pointed out some shortcomings of his techinque which combines host odour with an electrocuting net. For instance, nearly all the tsetse flies attracted to odour are in the later stages of the hunger cycle; catch levels may be affected by seasonal variations in the length of the tsetse hunger cycles and the availability of natural hosts; and the difficulty of interpreting the meaning of catch composition due to changes observed in catch composition as the quantity of host odour is increased. Finally, Dr. Vale identified desirable future improvements in sampling techniques, e.g. the isolation and identification of attractant host odours, and the design of newer traps which could work on conventional principles and which would be more economical or convenient than electrocuting nets. Presently, no traps exist whose efficiency can match that of large electrocuting nets, and these have potential application in studies of tsetse behaviour, epidemiology of trypanosomiasis, analysis of diet composition of the tsetse, and in novel methods of tsetse control (such as sterilization).

In the discussion that ensued, participants lauded Dr. Vale's significant contributions in tsetse sampling technique and generally suggested the experimental use of these electrocuting nets for studies of populations of other tsetse species in other parts of Africa. The question of cost was raised; and Dr. Vale disclosed that the total cost of the net plus battery was approximately US $20.00. Mr. Allsopp wondered what proportion of stunned tsetse recovered and escaped; but Dr. Vale stated that the use of a sticky material on the recovery tray at the base of the net ensured the trapping of each fly that received the electric shock. The practical implications of the repellent effect of human odour on the tsetse was stressed (Dr. McKelvey); and it was generally agreed that the characterization of the essential fractions of this odour should be pursued vigorously.

Dr. D.A.T. Baldry, drawing freely from his personal experience in Nigeria, discussed the "Ecological and Epidemiological Aspects of Atypical Tsetse Population." He reviewed literature on atypical populations of *G. tachinoides* in Nigeria where, in the eastern region, this species is intimately associated with the domestic pig as a result of which the fly's primary habitat coincides with villages. In such situations, *G. tachinoides* neither utilises riverine habitats nor shows much interest in biting man; it is also peridomestic in its resting, feeding and breeding behaviour. This is quite unlike *G. tachinoides* population in the northern region of Nigeria. An attempt to demonstrate cytotaxonomic differences between Nsukka populations of *G. tachinoides* (in the eastern region) and those in other parts of Nigeria proved negative. However, Dr. Baldry obtained morphological differences in the external genitalia of females of these two populations; and on the basis of this difference suggested that *G. tachinoides* in Nigeria is undergoing speciation. Finally, Dr Baldry reported cases of a typical populations of *G. palpalis* and *G. morsitans* in Nigeria, and discussed the epidemiological implications of these findings with regard to the almost total absence of human sleeping sickness as one moves south from the Niger/Benue valley.

In the discussion that followed, Professor Bursell cautioned that it might be premature to adjudge that due to their atypical ecology and habitats, the *G. tachinoides* populations of eastern Nigeria had indeed undergone speciation. However, it was generally agreed that due to the serious epidemiological implications of tsetse species becoming so closely associatetd with human habitation the ecology and behaviour of peridomestic tsetse populations deserves very close scrutiny. It was also generally felt that the genetics of tsetse species inhabiting ecologically different environments be given special attention so as to enhance our understanding of the basis for atypical "behaviour" of tsetse species.

Dr. S. K. Moloo in discussing "Interactions Between Various Components of the Zoonosis of African Trypanosomiasis in Infected Foci" reviewed the salient differences between the epizootiology of cattle trypanosomiasis and that of human trypanosomiasis respectively. Using Musoma District of Tanzania, he discussed various essential factors which interact in certain areas where trypanosomiasis is both endemic and enzootic and highlighted gaps in our current understanding of some of these essential factors. Surveys carried out by EATRO in collaboration with the Swiss Tropical Institute in 6 areas within this district, and where game and tsetse were abundant, revealed that:

1. Game animals function as a reservoir of *Trypanosoma brucei, T. congolense* and *T. vivax*.

2. Cattle and at least some game animals function as reservoirs of *T. rhodesiense*, infective to man

3. *G. swynnertoni* and *G. pallidipes* are vectors of *T. vivax, T. congolense* infections, and at least *G. swynnertoni* is a vector of *T. brucei*.

4. Cattle are exposed to challenge of the three trypanosome species; challenge due to *congolense* is more pronounced

5. There appear to be no restricted foci of Rhodesian sleeping sickness but rather the various components of zoonosis interact sporadically throughout this part of Tanzania.

Dr. Moloo then observed that the major obstacles to our full understanding of the manner in which the various essential components of the zoonosis of African trypanosomiasis in infected foci interact lie (a) in our present inability to quantify challenge, and (b) the absence of a productive surveilance method. He outlined the problems involved in removing these obstacles. These include among several others:

1. An acceptable definition of "challenge"

2. Possibility of non-involvement of the salivary gland in *T. brucei* transmission by the tsetse.

3. Refinement of methods of detecting trypanosomes in tsetse vectors.

4. Ascertaining the effect of game/tsetse relationships on trypanosome transmission.

In the discussion that followed, it was generally agreed by participants that investigations of tsetse/game interrelationships should be given priority.

SESSION ON TSETSE BEHAVIOUR

THURSDAY, 30TH SEPTEMBER, 1976

Dr. John Brady began his talk (on "Why Study Tsetse Behaviour in the Laboratory") by making a plea for more work to be done on the behaviour of tsetse flies in the field, and to relate this to basic studies in the laboratory. The fact that the *brucei* trypanosomes are transmitted primarily because of the behaviour of the tsetse flies suggests alternative tsetse control measures that would exploit weak links in tsetse behaviour. In order to consider such measures one must have through knowledge of tsetse behaviour.

A sequence of behaviour of flies in the field (rest — fly — approach — land — probe — engorge) is dependent on many variable stimuli and, therefore, it is difficult to to analyse the actual progress along the sequence of an individual tsetse fly. To remove the huge variables due to environmental factors, it becomes essential to look at the problem under more controlled condition in the laboratory.

The U-shaped activity curve for *G. morsitans* was always thought to be a response mainly due to temperature. However, when individual flies were studied in the laboratory, the U-shaped pattern of activity was found to occur independently of environmental change. Dr. Brady interprets this pattern to be an expression of the fly's endogenous circadian control of this behaviour, presumably sited in the fly's central nervous system.

Describing Pilson's observation and interpretation of field data by temperature-dependent activity thresholds (i.e. the lower activity threshold, about 18°C , below which no activity occurs and the higher threshold, about 32°C, above which the flies are inactive he argued that the explanation of a direct temperature correlation is not the whole story and that the endogenous circadian programme should also be considered. Analysing the data of some hourly catches of *G. morsitans* reported by Pilson and Pilson (1967) and Dean (1969), he showed that the U-shaped activity curve occurs independently of temperature. He emphasizes that in order to understand the tsetse fly activity pattern one must carefully consider both laboratory and field data.

Dr. Brady indicated that the daily activity pattern of female tsetse flies is similar to that of male flies, but he indicated that he had studied only a few females. He agreed that little is known regarding colours and shapes as visual stimuli and feels that more research is needed in this area. The importance of group behaviour, as a component of tsetse behaviour, was emphasized by some participants.

On a conclusion reached by a participant that basic laboratory work should be concentrated in the developed countries while field work is what the developing countries should engage in, Dr. McKelvey reacted strongly to such a suggestion, which he said was commonly expressed in certain quarters. Dr. McKelvey made the recommendation that, in addition to field work, there should be specialized laboratory work within the continent of Africa, and there should not be any reason to feel that basic research should always be done outside Africa. Professor Odhiambo fully supported this research strategy, and added that the fundamental questions in tsetse acoustic and mating behaviour are, in fact, in progress at the ICIPE where both laboratory and field problems are being considered simultaneously.

Professor Anthony Youdeowei, in his talk on "Feeding and Salivation Behaviour of Tsetse Flies," informed the participants that the salivation behaviour in tsetse has been little studied. This is mainly because of the difficulty of observing or recording the salivation process and the difficulty of collecting tsetse saliva. He described a technique which he developed for observing salivation and collecting saliva from tsetse flies during his tenure at the ICIPE. He offers individual tsetse stretched bat-wing membrane in a special apparatus. On making tarsal contact with the membrane, the fly probes, pierces the membrane, and then salivates. Using this method, it has been possible to study salivation behaviour both in the laboratory and in the field.

The actual feeding process includes two phases, namely piercing and gorging. The forward movement of the labium into the host's tissue is accompanied by a copious but intermittent outpouring of saliva from the hypopharynx. The entire feeding process is extremely rapid and may sometimes take only a few seconds (the so-called "capillary feeding") to a few minutes (termed "pool feeding"). How frequent capillary or pool feeding occurs is not known. Of particular intereset is the suggestion that if the feeding activity follows the U-shaped pattern, as Dr. Brady has proposed for activity in tsetse flies, then the salivation which involves parasite transmission during the peak biting periods of morning and evening stand a great chance of being more readily infected with trypanosomes than those which are available during the middle of the day when field biting activity is low.

Results of his studies on the composition of saliva and on salivation behaviour show that there is no difference between the physical appearance of saliva from an infected tsetse fly as compared to that from a non-infected fly. Using the bat-wing membrane technique, observations show that a tsetse fly can pierce and salivate many times. It is sugested that there is a continuous synthesis of saliva and its discharge into the lumen of the gland during the course of the feeding process. Copious salivation immediately following piercing will ensure that any trypanosomes present in the saliva will be effectively deposited into the tissue of the host. The first drop of saliva from an infected fly would be likely to transfer a larger quantity of trypanosomes to a host than would subsequent salivary secretions in a particular salivation sequence even though the fly may not succeed in actual engorgement. Thus, the first drop of saliva from an infected fly appears to be crucial in terms of parasite transmission. Professor Youdeowei indicated that more work is certainly needed before a definite conclusion can be reached about the effect of the presence of trypanosomes on the salivation behaviour of tsetse flies.

Several factors influence tsetse salivation, such as starvation, size of the fly, and sex of the fly. For example, the mean number of salivary drops secreted per minute and the mean size of the drops were increased with the increase in the intensity of starvation. It has also been shown that the larger the fly the larger the quantity of saliva secreted.

Studying the distribution of trypanosomes in the saliva, Professor Youdeowei posed the major question of how trypanosomes actually reach the salivary drops; and he suggested that the parasites may gradually pass down to the end of the proboscis and escape into the hypopharynx through the free end of the tip of the proboscis; alternatively, the parasite may simply accummulate around the tip of the proboscis when they mature so that when the haustellum labellum is subsequently rythmically inverted and everted during feeding in the tissues of the host the parasites simply escape into the tissue of the host simultaneously with the ejected saliva.

During discussion, it was indicated that the actual movement of the saliva is under a very specialised mechanism. The ultrastructure of the tube wall with particular reference to spirally arranged myofibrils on the terminal end, and the counter-acting connective tissue fibrils organized in the same region, as well as probable involvement of specialized nerve axons was discussed (Odhiambo). Additionally, it was indicated that the location and exact nature of the attachment of trypanosome parasites in the salivary gland is not yet understood although there is evidence to believe that the parasites located in the lumen and the duct are not necessarily intracellularly sited (Odhiambo). It was the consensus of the discussion that the salivation process which, in a real sense, is the common meeting ground for the vertebrate host, the parasite, and the vector should be one of the major areas of detailed studies in the future. Such an investigation should particularly consider the behaviour of trypanosomes in relation to salivation. Finally, the need for further studies on the salivary gland-based anticoagulant was emphasized.

Although from the biological and ecological point of view the house fly is quite different from the tsetse fly, Dr J. Keiding (including a contribution from Mr. K. Arevad) presented a paper on "Studies on the Resting Habits and Diurnal Activity of the House Fly as Related to Fly Control" in the hope that some of the principles may apply to tsetse flies.

Studies of the resting habits were conducted in a very simple manner, with no sophisticated or expensive equipment. The studies included observation of aggregations of flies and fly specks, counting of flies in rural and urban situations, both inside and outside buildings, the vertical distribution of flies, and similar investigations. Studies employing sticky tapes were also conducted in Danish piggeries and cow sheds.

The results showed that day-time activity included exploratory movements in search of food, moisture, mates and oviposition media. Flies were seen resting near sources of food, on animals in stables in temperate climates, and on the ground or floor in tropical and subtropical zones. Characteristic night resting sites were ceilings, edges of building structures, cords, wire, and similar structures in indoor situations particularly when vertically arranged, and shrubs, trees, narrow twigs and leaves, and low vegetation outdoors.

Experiments with suspended strips and tapes as artificial resting sites were conducted. These observations were made in stables or in large observation cages. Preference for vertical, dark, dry and rough surfaces were observed. Some experiments showed that newly emerged flies prefer a temperature of about 27°C whereas older flies prefer about 37°C. It was sugested that both visual and tactile stimuli, and perhaps also chemical ones are involved.

The novelty effect was studied in some detail. A new object, e.g. a black square, received more visits in the first few minutes after it was displayed to the flies than when it had become familiar to them after 15-20 minutes; secondly, the females were specially affected by this new object. Flies seem to have a memory lasting 5-10 minutes.

Laboratory studies on the orientation and resting of newly emerged flies were also conducted. Immediately after emergence from the puparium the teneral fly has a high spontaneous activity, which gradually decreases until the fly settles down and stretches its wings (15 minutes). Then follows a non-mobile period lasting 30-90 minutes (or more), after which the fly starts walking (which lasts for 2-6 hours), before it commences flight activity. The newly emerged active stage (with unstretched wings) always shows strong negative geotaxis and negative phototaxis, the geotaxis seems to be stronger than the phototaxis.

During discussion, Dr Keiding indicated that both visual and olfactory stimuli are probaly involved in the orientation of the preferred sites, and odour is perhaps only responsible for the short-range orientation. Dr Brady cautioned the users of laboratory olfactometers, since olfactometers create an unnatural and unrealistic situation for the test insects and therefore the data obtained from experiments conducted under such condition may be difficult to interprete correctly.

Resting behaviour has not been well investigated in the past, and almost nothing is known regarding tsetse night resting habits, nor are the components for selecting particular resting sites known. In order to understand this, a detailed investigation of the resting behaviour of tsetse is a necessity. It was also pointed out that very little is known regarding the behaviour of newly emerged teneral tsetse flies. Further research in this area is essential.

Mr Thomas Jaenson investigated various aspects of the mating biology of *G. pallidipes* under laboratory and field conditions ("Recent Studies on Mating Behaviour of *G. pallidipes*"). Study of female receptivity reveals that only about 10% of 1-3-day-old females are receptive. After day 3 there seems to be a gradual increase in the proportion of receptive females. A maximum receptivity level is reached on day 9 and maintained until day 14; thereofter, a decrease in receptivity level is noted.

One-day-old virgin females were paired with 14-25 day-old males every day until copulation occurred. Fifty per cent of females had copulated when 8-day-old. Relatively slow development of receptivity may also occur in a wild population as indicated by the dissection of young, non-teneral females from Kibwezi, Kenya. Under laboratory conditions, the increase in receptivity coincides with the attainment of maturity in follicle A and a decrease in duration of copulation.

Copulation involving 7-8-day-old females lasted 56 ± 20 min for flies from Kibwezi and 22 ± 6 min for those from Lambwe Valley, Kenya. Cross copulations of flies from the two populations showed that the male predominantly determines the duration of copulation.

F_1 and F_2 hybrid (Kibwezi × Lambwe) males copulate for about 35 min, a time period intermediate between the duration shown by the parental populations. This hybrid duration is highly significant when compared with those involving parental males. The variance is not significantly larger in copulations with F_2 hybrid males than those with F_1 hybrid males. Polygenes located mainly or only on the autosomes are presumed to determine the duration of copulation.

Mr Jaenson considers the following questions the most important for future research:

1. The nature of mating sites of various species of *Glossina* in the field
2. Whether multiple insemination occurs in the field
3. Studies on the genetic incompatibilities between different populations of the same tsetse species

4. Studies on the possible neuroendocrine control of male and female sexual behaviour.

Although Mr. Jaenson was able to achieve high insemination rate in his experiments, Dr Jordan reported that the Rhodesian strain of *G. pallidipes* does not seem to mate readily.

Citing examples from the work with blowflies, Dr Brady remarked that female receptivity seems to depend very much on her stage of nutrition with respect to protein input, and this phenomenon should be considered in studying tsetse mating behaviour.

It was generally agreed that investigations on genetic differences and incompatibilities between races and populations should be studied in detail not only with reference to vectorial capacity but with reference to mating and other aspects of behaviour as well.

Professor E. Bursell dealt with two aspects of the relation between energy reserves and activity ("Energy Reserves and Activity in Tsetse Flies") The first involved the interrelationship betwen the different types of energy reserve and the activity that they sustain, as expressed in intermediary metabolism. Pathways involved in the oxidation of proline had now been fully elucidated, but little was known about proline synthesis. Recent work using an *in vitro* system had confirmed that proline was capable of being synthesised by the fat body at rates which were substantial, though by no means adequate to reconstitute proline at the rate at which it is oxidised during flight. It was noted that a unique metabolic system was involved here, but that the possibility of taking practical advantage of this situation by attempting the development of specific insecticides should not be rated too highly, in view of the difficulties likely to be encountered in attempts to administer such insecticides to the insect under natural conditions.

The second aspect involved the quantitative relations between the different metábolic sources and "sinks" which had been made possible by the availability of calorific values for all of the components. On the basis of these, a balance sheet had been drawn up which showed that for the female tsetse the bloodmeal input was closely balanced by the corresponding respiratory, excretory and reproductive outputs, leaving only a small safety factor. These results confirm that interference with the input situation, e.g. by the slight reduction of host availability, might seriously interfere with reproductive potential. For the male tsetse, the balance sheet showed a very large surplus, indicating that the daily flight duration of 10 minutes which had been postulated for the purpose of drawing up the balance sheet might be a serious under-estimate. To account for the discrepancy, a daily flight duration of 50 minutes would have to be postulated, which would be contrary to current views on the pattern of activity in male tsetse flies.

During the discussion of Professor Bursell's paper, three main points emerged:

1. Tsetse flies depend mainly on proline metabolism, and have a life virtually without carbohydrates
2. The teneral flies use almost all of their initial bloodmeal intake for the purpose of building musculature
3. Most of the surplus energy in males is perhaps used during flight in searching for mates.

It was felt that studies are needed to understand more thoroughly the tsetse flight behaviour with particular reference to the mate searching behaviour and what proportional time it takes in the fly's life.

SESSION ON ECOLOGY, ECO-GENETICS AND BEHAVIOUR-RELATED TOPICS
FRIDAY, 1ST OCTOBER, 1976

In his paper on "Developments in Tsetse Genetics: Prospect and Retrospect", Dr W. Helle noted that detailed investigation of the genetic system of the tsetse fly was likely to remain beyond the bounds of practicality in view of the special features of the species' reproductive biology. He raised the question whether attempts to use subspecific or translocation-based sterility as a basis for control were of value. It was considered that genetical studies involving investigation of isoenzyme variation and chromosome morphology could contribute importantly in the study of genetic differences between subspecies and races of *Glossina* and in the detection of genetic differences between partially or completely isolated populations of a single species. The technique could also be used in guarding against the occurrence of undesirable genetic drift in inbred laboratory populations destined for use in sterile male release programmes.

In the next contribution, Dr L. P. S. van der Geest discussed the results of recent isoenyme studies on laboratory colonies of *morsitans* ("Experiences with Isoenzyme Studies on Tsetse Flies"). A variety of enzymes had been investigated. While a number had failed to exhibit substantial polymorphism, which was not surprising in view of extensive inbreeding, others had provided a reasonable degree of variation, and some had been successfully analysed in terms of the Hary-Winberg equilibrium. Using one of these appropriate enzyme systems, a comparison had been made between 5 different laboratory colonies, and large differences' in the relative frequency of different genotypes had been detected.

In applying the technique to field populations, it was noted the generally low level of genetic variability which appeared to characterise the species would be a drawback, as would the fact that enzymes of carbohydrate metabolism tended to be too feebly developed to be suitable for electrophoretic analysis.

In discussion, the suggestion was made that the technique might be capable of miniaturisation to the point where it would be unnecessary to sacrifice the flies from which samples were taken, thereby raising the possibility of performing crosses with known variants to elucidate details of the genetical basis of variation. The question of inbreeding in laboratory populations was raised; and it was noted that effects were unlikely to be serious in view of the fact that under normal conditions of laboratory maintenance inbreeding was never intensive.

Dr van der Geest also presented results on "Preliminary Studies on the Susceptibility of Pupae and Adults of *G. morsitans* to Some Insect Pathogens," including several species of fungi, two species of bacteria, and two species of nematodes. Tsetse pupae were generally found to be very resistant; but a small proportion of adults tested had been successfully infected with one of the fungal species, one of the species of bacterium had given 33% infection, and one of the nematodes 100% infection under the experimental conditions used, which had been specifically designed to maximise transmission. In the discusion that followed, attention was drawn to the desirability of including tests with insect viruses.

In the session following, Dr J. van Etten presented results of the first phase of studies on two isolated and geographically distinct populations of *G. pallidipes*, one from the Rift Valley of Kenya, and one from the coastal area near the border with Tanzania ("Comparative Studies on Two Semi-isolated Populations of G. pallidipes"). In the field, differences between the two populations had been demonstrated in respect of their responses to different sampling systems, in the pattern of their diurnal activity, in the fat content of adult flies, and in the incidence of pupal parasitism.

In the laboratory, colonies derived from the two populations had been established. Differences between them had been demonstrated in respect of mortality during early adult life, in respect of the proportion of surviving females which were reproductively active, and in the feeding behaviour. The results of fractionations of lipids extracted from field flies had been of special interest in showing remarkably high proportions of cholesterol esters, sometimes exceeding 80% of total lipid.

In the discussion that followed, doubts were expressed whether the differences which had been demonstrated between the two populations in the field were really the expresison of differences between the two populations, rather than of the difference between the two different environments, especially in view of the fact that all of the parameters tested are known to show extremely strong environmental interactions. However, it was accepted that the differences which appeared to characterise laboratory colonies derived from the two populations provided evidence of a real population difference; and it was noted that isoenzyme studies would be undertaken in an attempt to provide further evidence of the existence of genetic differences. It was suggested that the game situation and tsetse feeding patterns might be usefully explored, and that an attempt should be made to analyse the data on diurnal activity patterns in such a way as to separate environmentally and endogenous components, as described in an earlier contribution by Dr. Brady.

The afternoon session was opened by Dr S. N. Okiwelu, who described the general tsetse situation in Zambia, and presented results relating to the resting sites of *G. morsitans* and to seasonal variations in the rate of abortion ("The Monthly and Seasonal Fluctuations of Suspected Abortion Rates in a Natural Population of *G. m. morsitans* in the Republic of Zambia").

In studying the resting sites of tsetse flies, use had been made of a sticky substance ("tangle-foot") in resting sites, which served to trap the flies which landed on them. By this method, it had been shown that holes of trees were the most favoured resting sites; that flies resting here, as with those resting at the top of bush or tree canopies, showed a negative correlation between catch and height, with few flies being caught at heights above 5 meters. Shaded logs and bushes were favoured during the hot dry season, but ant-bear holes were seldom used even at the height of the dry season.

The method of Madubunyi had been used to assess seasonal changes in the incidence of abortion during two successive years. In the first year, the rate of abortion had been low during the rainy season, increasing through the cool dry season to a peak in the hot dry season. In the following year, the abortion rate during the hot dry season had shown a decrease instead of an increase consequently, it had become clear that results would be incapable of simple interpretation.

Dr Madubunyi discussed existing views on "The Role of Food in Tsetse Population Dynamics." He reported that abortions occurred with increasing frequency towards the end of the rainy season in a natural population of *G morsitans morsitans* which he studied in a game reserve in Central Zambia between 1972 and 1973. He pointed out that this evidence of the occurrence of nutritional stress during a season when conditions are supposed to be almost ideal for the tsetse and its wildlife hosts, clearly illustrates the urgent need for a critical quantitative evaluation of tsetse/host relationships. He reviewed conditions under which tsetse abundance could be dependent on its hosts' abundance and examined possible pathways of tsetse/host population interaction, including the direct and indirect effects of competition from other haematophagous Diptera in precipitating nutritional stress. He sugested a team approach to future investigations of not only the role of food in tsetse population dynamics but also all other aspects of tsetse ecology, involving entomologists, wild life ecologists, parasitologists, systems analysts and epidemiologists.

Participants endorsed the multi-disciplinary approach to studies of tsetse ecology and expressed optism that a combination of Dr Madubunyi's novel technique for detecting abortions in wild female tsetse and Dr Vales' electrocuting traps which catch a higher proportion of females that any other existing sampling method will go a long way in providing answers to some unknowns about tsetse population regulation with particular reference to the role of food.

The importance of a multi-disciplinary approach to the problem of tsetse ecology was stressed again in a subsequent communication by Mr R. Allopp, who pointed also to the need for a broader evaluation of tsetse and trypanosomiasis control in the general context of the management of natural resources.

In the last communication of the afternoon, Dr E. D. Offori ("Maintenance of Tsetse Flies in the Laboratory: Some Practical considerations") described a number of ways by which current practices could be streamlined in such a way as to provide more effective use of available resources.

In the evening session, Dr L. Wililams provided an illustrated review of progress in the sterile-male release programme at Tanga, Tanzania; and this was followed by a review by Mr Allsopp of the tsetse situation in Botswana.

EVALUATION OF WORKSHOP DISCUSSIONS

SATURDAY, 2ND OCTOBER, 1976

The morning session of Saturday, the 2nd October 1976, was devoted to a general discussion, based on the outlines prepared by the rapporteurs from the deliberations and discussions of the entire Study Workshop. The outlines were presented to the participants as research priorities on tsetse ecology and behaviour, and were as follows:

Wednesday; 29th September, 1976

1. Multidisciplinary investigations of tsetse/host/parasite interrelationships leading to systems analysis. Particular attention to be paid to factors affecting mortality of tsetse and transmission of parasite

2. Host odours and pheromones: identification of active components and evaluation of potential for practical applications, e.g. of improved trap performance for sampling of low density populations or for sterile-male programme based on capture/release

3. Atypical tsetse populations: investigation of possible genetic basis of shift in feeding and other behaviour patterns, and of the possibility of reducing challenge by management practice.

Thursday, 30th September, 1976

1. Integrated laboratory/field investigation of tsetse behaviour, including
   - Social behaviour
   - Mating behaviour
   - Response to host animals
   - Flight behaviour
   - Behaviour of newly emerged tenerals

2. Physiology of salivation, with special reference to the possibility of interfering with trypanosome transmission

3. Investigations of genetic differences and incompatibilities between races and populations, with special reference to vectorial capacity

4. Investigation of tsetse/host interrelationships, with special reference to nutritional stresses and reproductive potential.

Friday, 1st October, 1976

1. Intensification of isoenzyme studies with special reference to the study of genetic differences between geographically or behaviourally distinct populations of various species of tsetse

2. Multidisciplinary studies of tsetse/host interrelationships, with special reference to nutritional stress and possible effects on reproductive performance

3. Behavioural studies of the "intermediate-range" reactions of tsetse flies to their hosts

4. Investigations of the role of parasites, predators and pathogens as agents of tsetse mortality

5. Consideration of tsetse control in the broader context of land management, and of the research required to provide a sound basis for evaluation.

GENERAL DISCUSSION

Although multidisciplinary investigations of tsetse/host/parasite interrelationships is not desirable, it was felt that the best course would be to look at segments of the complex separately, and think, for instance, in terms of (a) a population model for tsetse alone and (b) a separate epidemiological model. A tsetse population model should particularly consider nutritional stress, reproductive potential, and the quantitative aspect of various mortality factors.

The research on regulatory pheromones should also include the evaluation of their use in conventional control as well as in autosterilization situations. Need for the development of better sampling methods for low-density populations was stressed throughout the meeting.

Discussing the need of research on atypical tsetse populations, it was pointed out that particular attention should be given to the domestic situation, such as human ecology, live stock management practices, agricultural practices and their influences on host and fly distribution and density and host/fly contact. Necessity for investigating the peridomestic tsetse population was stressed.

So far there has been little integration between laboratory and field studies of tsetse behaviour, and the need was emphasized of a more detailed integrated laboratory/field investigation of tsetse behaviour, with particular reference to the behaviour of tenerals, mating behaviour, responses to hosts, flight behaviour and resting behaviour.

Although many aspects of vector trypanosomes relationship are now becoming clearer, there is still need for research on the physiology of salivation and salivary glands with particular reference to the trypanosomes pathways within the vector.

Although there is existing research on tsetse isoenzyme, it was felt that intensification of isoenzme studies with reference to the study of genetic differences between geographically isolated and behaviourally distinct populations of different species of tsetse should be considered.