*Journal of the American Mosquito Control Association*, 10(2):258–265, 1994

# THE TSETSE (DIPTERA: GLOSSINIDAE) STORY: IMPLICATIONS FOR MOSQUITOES

S. J. TORR

*ODA Insect Pest Management Initiative, % Tsetse Control Branch,*
*P. O. Box 8283, Causeway, Harare, Zimbabwe*

ABSTRACT. In Zimbabwe, tsetse flies (*Glossina* spp.) are controlled using insecticide-impregnated baits. About 60,000 targets, baited with a blend of acetone, 1-octen-3-ol, 4-methylphenol, and 3-n-propylphenol, are deployed in tsetse-infested areas. The development of this control technology has been based on an understanding of the responses of tsetse to their hosts, using research tools that quantify single specific responses. This understanding required the development of new research tools, such as electrocuting devices and video techniques to analyze behavioral responses and gas chromatography linked to an electroantennogram to analyze responses of tsetse to components of host odor. The development of bait technology also required close interdisciplinary collaboration among entomologists, chemists, and electrophysiologists. It is suggested that the same approach to analyzing the responses of mosquitoes to their hosts will produce improved baits for mosquitoes. The low reproductive rate of tsetse, their sensitivity to insecticides, and, so far, the absence of insecticidal or behavioral resistance to insecticide-impregnated targets, makes them particularly susceptible to baits. These factors are not all present with other pests, including mosquitoes. Nonetheless, baits offer the prospect of being an important component in an integrated approach to controlling pests of man and his livestock, both as a complementary control technique and as a powerful monitoring tool.

## INTRODUCTION

Tsetse flies (*Glossina* spp.) occur over some 11 million km$^2$ of Africa, covering 37 countries, where they transmit various species of *Trypanosoma* that cause animal and human trypanosomiasis. The human disease threatens some 45 million people and their livestock, including about ⅓ of the 150 million cattle in tropical Africa (Jordan 1986). In cattle the disease produces loss of condition, anaemia, abortions, sterility, and if untreated, death. In Zimbabwe about half the country has suitable habitat for tsetse, although today only some 30,000 km$^2$ are infested. The Zimbabwe Tsetse and Trypanosomiasis Control Branch prevents tsetse from expanding out of this area and aims to eradicate tsetse from the country.

In Zimbabwe, at the beginning of the 1980s, tsetse control was effected by drift-spraying tsetse-infested bush with insecticides from aircraft, or by spraying the resting sites of tsetse. Both techniques have an impact on nontarget species, are expensive, and are logistically complex. Today these techniques have been replaced completely in Zimbabwe by the use of insecticide-impregnated baits. The baits are either targets, which consist of panels of cloth that are impregnated with insecticide and odor baited with a blend of acetone, 1-octen-3-ol (henceforth termed octenol), and phenols, or cattle dipped with a formulation of deltamethrin that is active against both ticks and tsetse. Tsetse are attracted to the baits by a combination of visual and olfactory stimuli and pick up a lethal dose of insecticide when contacting the bait. Targets deployed at densities of 4/km$^2$ kill about 3% of the female tsetse population a day. The low reproductive rate of tsetse means that the relatively low mortality rate exerted by the targets is sufficient to eradicate a tsetse population within a year. The technique does not appear to affect nontarget species, it is cheaper than alternative techniques, and is less demanding logistically (Vale et al. 1988b). The dramatic change in the techniques used to control tsetse is the result of a revolution in our understanding of tsetse biology, in particular how tsetse locate their hosts.

## ELECTRIC NETS

Until the 1970s, field studies of tsetse used traps or fly rounds. The latter consisted of a party of men walking through the bush, sometimes carrying a screen of black cloth, or walking with an ox. The men used handnets to catch tsetse that they saw alighting on the screen or the ox. The samples thus caught showed a preponderance of males over females, young flies over old ones, and in Zimbabwe where *Glossina pallidipes* Austen and *Glossina morsitans morsitans* Westwood are frequently sympatric, a preponderance of *G. m. morsitans* over *G. pallidipes.* Conversely, the designs of tsetse traps then in use caught relatively small numbers of tsetse but with greater proportions of females, old flies, and *G. pallidipes.* To investigate the cause of these differences, Vale (1974a) attempted to sample all the flies approaching a natural host by surrounding it with a ring of electric nets.

The electric net consists of a panel of fine black netting sandwiched between 2 grids of electrocuting wires 0.2 mm thick and 8 mm apart (Vale 1974b). These grids are virtually invisible to tsetse. Tsetse approaching the ox collided with the nets, were killed or stunned, and fell onto sticky trays where they were retained. Vale showed that the sex, age, and species biases obtained with man-fly rounds were artifacts of the sampling system. If a man was placed in the ring of nets the composition of tsetse caught on the nets resembled that obtained with the man-fly round. In the absence of man the catch showed a preponderance of *G. pallidipes,* females, and older flies. This experiment also showed that more tsetse were caught on the downwind side of the ring, suggesting that tsetse were responding to host odors. Previously, although it was suspected that tsetse employed odors to locate their hosts, it was generally thought that visual cues were more important (Bursell 1961).

Vale went on to carry out a series of elegant experiments where he separated the cues that may be responsible for attracting tsetse. Several studies hid live animals in roofed pits from which odors were exhausted at ground level via a fan (Vale 1974a). Hence it was possible to compare, for example, the numbers of tsetse attracted to a warthog, a visual model of a warthog, or just the smell of a warthog. The results showed that some 90% of tsetse attracted to a host did so in response to the host's odors. It was also possible to compare the responses of tsetse to odors from various types and numbers of hosts, different parts of a host, and hosts in different physiological conditions. It transpired that the numbers of tsetse attracted to a host were positively correlated with the body mass of the host. Ten-fold increments in the body mass of hosts resulted in a *ca.* 2.5-fold increase in the catch; this dose response continued up to at least a body mass of 11,500 kg of hosts (Hargrove and Vale 1978). Population models of tsetse suggested that efficient traps deployed at densities of just 1 trap/10 km$^2$ and baited with such an odor could eradicate tsetse populations.

During the 1970s, random screening of chemicals led to the identification of carbon dioxide and acetone as active components of host odor. In the 1980s, collaboration with chemists and electrophysiologists from the Natural Resources Institute in the United Kingdom led to the identification of octenol, butanone, and a number of phenols as attractants.

The *Morsitans* Group of flies appears to show the most highly developed responses to host odors. In contrast, the *Palpalis* Group of flies, generally found in riverine situations in West Africa, shows only a slight (Mérot et al. 1986) or no response to host odors (WHO 1986). There is also some evidence of intraspecific differences in the responses of tsetse to host odors; *G. pallidipes* in Somalia appear to be less responsive than the same species in Zimbabwe (Torr et al. 1989).

## HOST-ORIENTED RESPONSES OF TSETSE

Much work has been carried out to elucidate how tsetse use olfactory and visual stimuli to locate their hosts. Studies have been made of the behavior of tsetse from the initial contact with host stimuli to final location of a host and we now have a broad idea of the behavioral mechanisms involved.

*Initial contact:* Tsetse are only active for <30 min a day, typically during early morning and late afternoon (Hargrove and Brady 1992). For the rest of the time, tsetse rest on tree branches and boles, or in refuges such as tree rot holes in the hot dry season when temperatures exceed 32°C (Vale 1971). Torr (1988a) studied the responses of tsetse in refuges to natural and synthetic olfactory and visual stimuli and found that flies responded to a moving visual stimulus similar to a host walking past the refuge and to a stimulus of 100% ox odor and 0.08% carbon dioxide. There was no significant response to 25% ox odor, acetone, or octenol. Most flies left the refuge in the apparent absence of any host stimuli, presumably in response to an endogenous activity rhythm (Brady and Crump 1978) modulated by nutritional condition (Randolph and Rogers 1978, Hargrove and Packer 1993) and exogenous environmental stimuli such as temperature (Vale 1971, Torr 1988a) and falling light intensity (Brady 1987). Hence tsetse appear to hunt actively for hosts rather than wait for a passing host, except when stimulated by olfactory or visual stimuli from a nearby host.

Video studies of tsetse flying in the apparent absence of any host stimuli, and presumed to be ranging in search of a host, showed that tsetse fly with a downwind bias (Gibson et al. 1989). Other studies show that ranging tsetse fly towards hostlike objects, flying to the downwind side of the object where olfactory stimuli may be used to distinguish hosts from inanimate but attractive objects such as stumps or fallen trees (Vale 1991). If the object is not a potential host and there are no olfactory stimuli tsetse then fly toward other nearby attractive objects or crosswind (Torr 1989).

*Odor-oriented behavior:* Eventually, ranging tsetse may encounter a plume of host odor, and on entering it they then turn upwind (Gibson and Brady 1988). Laboratory studies (Colvin et al. 1989) have shown that tsetse can assess wind direction by the visual cues produced by wind drift (i.e., optomotor-mediated upwind anemotaxis). Tsetse in an odor plume fly at <0.5 m (Torr 1988b) above the ground at 6 m/sec (Gibson and Brady 1985, 1988; Gibson et al. 1989) and are oriented generally upwind (Vale 1974a; Gibson and Brady 1985, 1988; Torr 1988b). If tsetse fly out of an odor plume, they execute a reverse turn to bring them back in contact with the plume, and on regaining contact they reorient upwind (Gibson and Brady 1988, Torr 1988b). Field studies of the responses of tsetse to components of host odor indicate that carbon dioxide alone elicits upwind anemotaxis but the other known components elicit little or no directional response (Torr 1988c, 1990). At low concentrations there is no directional response to carbon dioxide unless acetone or octenol are also present (Bursell 1987, Torr 1990). Studies using electric nets placed at various distances downwind of a host show that a plume of odor from a single ox elicits upwind flight 90 m downwind of the source (Vale 1977a) and studies using odors from 60 tons (approximately a body mass of 53,000 kg) of cattle suggested that tsetse were responding 400–600 m downwind (M. T. P. Holloway, unpublished data).

Laboratory and field studies indicate that tsetse take off upwind when stimulated by host odor. This led Bursell (1984a, 1987) to suggest that tsetse also assess wind direction on the ground and then progress upwind in a series of steps, taking off upwind in the presence of odor and landing when odor is lost. Laboratory and field studies employing video techniques also suggest that natural and synthetic host odors reduce flight speed (orthokinesis) and increase the rate of turning in tsetse (klinokinesis) (Gibson et al. 1989, Warnes 1990). Studies of air movement in typical tsetse habitat (Brady et al. 1990) suggest that odor from a host does not move in straight lines from the host, hence a notional tsetse flying directly upwind at just 5 m downwind would frequently be flying at >90° away from the host direction. This problem will be exacerbated at 50–100 m such as might occur in plumes of ox odor. The quality of the directional information provided by a plume of odor varies according to wind speed, topography, and habitat, the problem being severest in thick bush and at low wind speeds. Thus, the relative importance of the in-flight and hopping tactic mechanisms and the kinetic responses may vary according to changes in wind speed and habitat. For example, where directional information is poor then the kinetic mechanisms may be more important. Recent studies have shown that tsetse navigate up odor plumes by flying along game trails (Paynter and Brady 1992). In these situations tsetse may simply have to gauge the wind direction only very roughly, that is, up- or downtrail. Thus, the problem of determining source direction in thick bush may not be as serious as Brady et al. (1990) first suggested.

As tsetse progress up the plume they divert to nearby visual targets. Studies of the interaction of visual and olfactory stimuli suggest that the probability of diverting from upwind flight to an object is modulated by the color and shape of the object. The propensity to divert to variously colored targets decreases in the order: black = blue > red > yellow (Green 1986, Torr 1989) and for different shapes it decreases in the order: circle > square > horizontal oblong = vertical oblong (Torr 1989). Hence, flies are more likely to divert toward a dark compact object such as a warthog rather than a tree bole. Changes in the odor composition or concentration or loss of contact with odor do not affect the proportion of tsetse that divert to an object. The rules of thumb for distinguishing hosts from other objects occasionally cause tsetse to diverting to inanimate objects, such as a fallen log (Vale 1991). In this event tsetse fly briefly round the object and then continue flying upwind, if the object lies within the odor plume, or crosswind if it lies outside the plume (Torr 1989). The crosswind flight presumably maximizes the probability of tsetse reencountering the odor plume.

Eventually the tsetse comes within visual range of the host producing the odor and homes in on visual cues. Landing on the host is modulated by olfactory and visual stimuli. The propensity to land is greater on vertical oblong shapes than on horizontal ones (Vale 1974a, Torr 1989) and greater in the presence of complete natural ox odor or carbon dioxide (Vale and Hall 1985). The host's grooming is important in controlling the proportion of tsetse that alight (Vale 1974a), the alighting site (Torr, unpublished data), and the percentage of tsetse that feed (Vale 1977b).

## PRACTICAL APPLICATION

Following extensive studies of the host-oriented responses of tsetse by Vale and his colleagues, improved designs of trap and target were developed. In 1983, tsetse were eradicated from a small island on Lake Kariba using simple insecticide-impregnated targets, baited with acetone and octenol (Vale et al. 1986b). The following year some 2,500 targets were deployed over an area of 600 km$^2$. Within 9 months tsetse were eradicated from the center of this area and their numbers reduced by >95% at the edges (Vale et al. 1988b). Today some 60,000 targets are deployed elsewhere in Zimbabwe to control tsetse (V. Chadenga, unpublished data).

Since those first large-scale trials in 1983–84, simpler, cheaper, and more effective targets have been developed. The identification of phenolic attractants doubled the efficacy of targets (Vale et al. 1988a) and further improvements have been made in their design (Vale 1993a). Improved means of dispensing attractants have been developed where the odors are released by diffusion through sealed polythene sachets, giving a slow and controlled release of attractants for more than a year (Hall et al. 1992) and the effective life of the insecticide applied to the target has been increased from 3 to >15 months (Torr et al. 1992).

The technique can still be improved. Comparisons of synthetic and natural ox odor show that the catch of the synthetic blend is only half that of the natural one, suggesting that unidentified attractants are present in ox odor that can at least double the efficacy of the present targets (Torr and Hall, unpublished data). Further improvements are likely to arise from an enhanced understanding of the effect of site on trap and target performance and in optimizing the deployment pattern of targets (Hargrove 1993).

## IMPLICATIONS FOR MOSQUITO CONTROL

The development of baits for tsetse and our current understanding of how tsetse use host stimuli hold implications for the development of baits for mosquitoes and other pests.

*Value of basic research:* The most important lesson from the tsetse story is the value of understanding the basic behavioral responses of tsetse. Interest in using traps to control tsetse has existed for much of this century and a huge amount of empirical work has been carried out comparing the catches of different designs of trap and odors. This work produced traps that caught more tsetse but, in general, the technique did not eradicate populations of tsetse and consequently interest in traps dwindled. The basic research by Vale and Hargrove in the early 1970s showed that most tsetse arriving at a stationary host did so in response to host odors, that existing designs of trap were <10% efficient, and that human odors were repellent to tsetse. These findings showed that traps could be substantially improved by: 1) identifying the attractants present in ox odor, 2) designing efficient traps and targets, and 3) developing research techniques that could be used in the absence of man. The research techniques needed to measure single specific and instantaneous responses in an objective and quantitative manner.

As Vale (1993b) has recently pointed out, a proper understanding of tsetse behavior relied on the ability to isolate single stimuli and responses. Failure to do so can lead to spurious conclusions. For instance, consider an experiment to study the responses of tsetse to different colors by comparing the catches of tsetse from traps colored black, white, blue, and red. The catches would decrease in the order blue, white, red, and black (Green and Flint 1986) and we might have concluded that tsetse were not attracted to black objects. In fact, black along with blue is the most attractive color but unlike blue it also elicits a strong landing response. Hence tsetse attracted to the black trap land on the outside of the trap and are not caught. The problem has arisen because the 'response' measured by the traps (i.e., the number of flies caught by the trap) is a combination of several different responses (e.g., approaching the trap, landing on the outside, entering it). For tsetse workers, understanding this difference has led to insecticide-impregnated targets being largely black, because here the tsetse are attracted to the target and induced to alight on it and pick up a lethal dose of insecticide. However, traps for tsetse are externally blue, to maximize the numbers attracted to the vicinity, with black internal surfaces to increase the proportion of tsetse that enter the trap (Vale 1983a, Flint 1985).

This type of result is not unique to tsetse. Comparisons of the numbers of New World screwworm (*Cochliomyia hominivorax* (Coquerel)) caught in different colored traps led to the conclusion that they were more attracted to yellow traps than black ones (Peterson 1982). Recent studies with electric nets (Torr and Hall 1992) showed that adult screwworms were attracted to differently colored targets in equal numbers but black elicited a stronger landing response. Presumably the poor performance of the black trap was because the flies alighted on the outside of the trap instead of entering it.

*Techniques:* Analysis of the host-oriented behavior of tsetse has depended on the development of new research tools. Electrocuting devices and video techniques have enabled us to separate various types of response such as flight direction and landing. The ventilated pit and its variants allowed separation of visual and olfactory stimuli and fractions of olfactory stimuli and the linked gas chromatograph–electroantennogram (GC-EAG) (Moorhouse et al. 1969, Hall et al. 1984, Cork et al. 1990) enabled individual olfactory components to be isolated and analyzed to determine which chemicals elicited an electrophysiological response. Some of these techniques, such as ventilated pits and the GC-EAG can be readily and profitably applied to studies on mosquitoes. One of the most challenging areas is the need for a field device equivalent to the electric net for tsetse that is applicable to mosquitoes. Video techniques undoubtedly go some way to meeting this need but they do not allow precise identification of the species being viewed, especially in studies of sibling species such as the *Anopheles gambiae* complex. Modification of the electric net merits serious consideration as a tool for sampling mosquitoes.

A problem in the search for tsetse attractants has been that different field and laboratory techniques have given different indications of activity. This arises in part from different odors having different behavioral effects. For instance, acetone and octenol have an effect on flight orientation but do not activate flies and, conversely, carbon dioxide at low concentrations activates tsetse but does not elicit a directional response. Hence field or laboratory assays based on, say, just one of these responses would not identify all of these odors as attractants (Bursell 1987, Torr 1990). Some odors appear to increase the numbers of flies that enter traps but have no effect on the numbers of tsetse attracted to the vicinity of the bait. Such odors therefore increase the catch of traps but have no effect on the catch of electric targets (Vale et al. 1986a, Torr et al. 1989). One solution to this problem is to carry out a wide range of separate studies on, for example, activation, flight direction, flight speed, and rate of turning. A more elegant solution is to develop an assay that incorporates a large number of different behavioral responses where each of these responses can be measured separately. For instance, Warnes and Green (1992) measured activity, flight speed, rate of turning, and flight direction in New World screwworm flies in a laboratory assay of wound odors. And in the field, Vale (1983b) developed an assay that simultaneously measured the numbers of tsetse attracted to a bait, their landing responses, and flight direction.

A 2nd problem in the search for tsetse attractants has been the conflicting indications of laboratory and field techniques. For instance, 2-methoxyphenol, a component of ox urine, elicits upwind flight in a wind tunnel (Bursell et al. 1988) but in the field it is a potent repellent (Vale et al. 1988a). This underlines the importance of field studies to verify that laboratory assays are faithfully portraying natural responses.

*Integrated studies:* The development of bait technology requires close interdisciplinary collaboration. For instance, the identification of octenol arose from field entomologists identifying ox breath as a natural source of attractants (Vale 1974a), chemists and electrophysiologists identifying the physiologically active components within ox breath (Hall et al. 1984), laboratory entomologists demonstrating that the component was behaviorally active (Bursell 1984b), field entomologists determining the responses of tsetse to octenol alone and in combination with other attractants (Vale and Hall 1985), and chemists developing cheap and practical methods of dispensing octenol (Hall et al. 1992).

*Type of bait:* In developing a bait system for controlling tsetse, workers in Zimbabwe have concentrated on studying the responses to natural hosts. Twenty years after Vale first started looking at these responses, the blue-colored traps and the 4 chemicals that we now use to survey and control tsetse bear little obvious relation to a natural host of tsetse, such as a warthog, one of the hosts that Vale (1974a) first studied. However, the baits in use today are essentially a distillation of all the attractive features of the host. Repellent stimuli that are inherently part of the host have been removed and the attractive cues accentuated. Hence, 2-methoxyphenol and lactic acid, upright forms, and yellow coloration are absent in the artificial bait but present in natural ones. Conversely, attractive host stimuli such as blue coloration, horizontal form, and the various semiochemicals are accentuated in the synthetic bait.

There are a large number of studies showing that baiting traps with whole natural host odor or some components of host odor increases the catch of mosquitoes. For instance, carbon dioxide (Gillies 1980), L-lactic acid (Acree et al. 1968), and octenol (Takken and Kline 1989) increased the catch of mosquitoes from a light trap. These findings have been important in providing a powerful stimulus to developing a bait system for mosquitoes. However, there is clearly no relationship between, for example, a CDC trap and a host, and it is not clear what precise behavioral effect the host odors exert. It now seems timely to direct attention away from studying the effect of odors on trap catches and toward the responses of mosquitoes to their natural hosts, using the methods and tools outlined above. Such work will identify the attractive and repellent components present in a host and this information can then be used to develop effective bait systems.

*Prospects for success:* The development of odor baits to control tsetse is perhaps the best example of the use of kairomones to control a medical and veterinary pest. Much of this success is due to the biological peculiarities of tsetse. Its low reproductive rate makes it particularly susceptible to a low and continuous mortality such as that caused by odor-baited targets (Hargrove 1988). It is an obligate bloodfeeder and every 2–3 days male and female tsetse must visit a host. Hence, tsetse is repeatedly available to odor baits. Tsetse are particularly sensitive to insecticides, being, for example, >100 times more susceptible to deltamethrin than the New World screwworm and thus a fleeting contact with an insecticide-impregnated bait is lethal (Torr 1985, Harris et al. 1991). There has never been any record of tsetse developing insecticidal or behavioral resistance despite some populations in Zimbabwe being subject to 9 years of continuous exposure to insecticidal targets with massive immigration into the area and exposure to sublethal doses of insecticide—factors most likely to produce resistance (Maudlin et al. 1981).

The population biology and physiology of many other insect pests may make the use of odor baits less suitable as a control measure. However, bait systems can provide a powerful supplement to other techniques, as for example in the use of baits to control New World screwworm flies (Snow et al. 1982, Mackley and Brown 1987). Moreover, the development of improved monitoring and sampling systems, based on an improved understanding of host-oriented behavior, will enhance greatly the rational management of insect pests of man and livestock.

## ACKNOWLEDGMENTS

I thank R. J. Phelps, G. A. Vale, D. R. Hall, M. L. Warnes, J. W. Hargrove, and P. Shaw for much useful discussion and helpful comments on an earlier draft, and the United Kingdom Overseas Development Administration for financial support. The paper is published with the permission of the Assistant Director, Department of Veterinary Services (Tsetse and Trypanosomiasis Control) Zimbabwe, and the Director, Natural Resources Institute, United Kingdom.

## REFERENCES CITED

Acree, F. B., H. K. Turner, M. Gouck and C. N. Smith. 1968. L-lactic acid: a mosquito attractant isolated from humans. Science 161:1346–1347.

Brady, J. 1987. The sunset activity of tsetse flies: a light threshold study on *G. morsitans*. Physiol. Entomol. 12:363–372.

Brady, J. and A. J. Crump. 1978. The control of circadian rhythms in tsetse flies: environment or physiological clock? Physiol. Entomol. 3:177–190.

Brady, J., G. Gibson and M. J. Packer. 1990. Odour movement, wind direction and the problem of host finding by tsetse flies. Physiol. Entomol. 14:369–380.

Bursell, E. 1961. The behaviour of tsetse flies (*Glossina swynnertoni* Austen) in relation to problems of sampling. Proc. R. Entomol. Soc. Lond. (A) 36:9–20.

Bursell, E. 1984a. Observations on the orientation of tsetse flies (*Glossina pallidipes*) to wind-borne odours. Physiol. Entomol. 9:133–137.

Bursell, E. 1984b. Effects of host odour on the behaviour of tsetse. Insect Sci. Appl. 5:343–349.

Bursell, E. 1987. The effect of wind-borne odours on the direction of flight in tsetse flies. Physiol. Entomol. 12:149–156.

Bursell, E., A. E. J. Gough, P. S. Beevor, A. Cork, D. R. Hall and G. A. Vale. 1988. Identification of components of cattle urine attractive to tsetse flies *Glossina* spp. (Diptera: Glossinidae). Bull. Entomol. Res. 78:281–291.

Colvin, J., J. Brady and G. Gibson. 1989. Visually guided, upwind turning behaviour of free-flying tsetse flies in odour-laden wind: a wind tunnel study. Physiol. Entomol. 14:31–39.

Cork, A., P. S. Beevor, A. J. E. Gough and D. R. Hall. 1990. Gas chromatography linked to electroantennography: a versatile technique for identifying insect semiochemicals, pp. 271–279. *In:* A. R. McCaffery and I. D. Wilson (eds.). Chromatography and isolation of insect hormones and pheromones. Plenum Press, New York.

Flint, S. 1985. A comparison of various traps for *Glossina* spp. (Glossinidae) and other Diptera. Bull. Entomol. Res. 75:529–534.

Gibson, G. and J. Brady. 1985. 'Anemotactic' flight paths of tsetse flies in relation to host odour: a preliminary video study in nature of the response to loss of odour. Physiol. Entomol. 10:395–406.

Gibson, G. and J. Brady. 1988. Flight behaviour of tsetse flies in host odour plumes: the initial response to leaving or entering odour. Physiol. Entomol. 13: 29–42.

Gibson, G., M. J. Packer, P. Steullet and J. Brady. 1989. Orientation of tsetse flies to wind, within and outside host odour plumes in the field. Physiol. Entomol. 16:47–56.

Gillies, M. T. 1980. The role of carbon dioxide in host-finding by mosquitoes (Diptera: Culicidae): a review. Bull. Entomol. Res. 70:525–532.

Green, C. H. 1986. Effects of colours and synthetic odours on the attraction of *Glossina pallidipes* and *G. morsitans morsitans* to traps and screens. Physiol. Entomol. 11:411–421.

Green, C. H. and S. Flint. 1986. An analysis of colour effects in the performance of the F2 trap against *Glossina pallidipes* and *G. morsitans morsitans* Westwood (Diptera; Glossinidae). Bull. Entomol. Res. 76: 409–418.

Hall, D. R., P. S. Beevor, A. Cork, B. F. Nesbitt and G. A. Vale. 1984. 1-Octen-3-ol: a potent olfactory stimulant and attractants for tsetse isolated from cattle odours. Insect Sci. Appl. 5:335–339.

Hall, D. R., A. J. E. Gough, P. H. Adams, P. S. Beevor, A. Cork, C. H. Green, J. L. Smith, J. H. L. Taylor and M. L. Warnes. 1992. Identification of host odour attractants for tsetse flies: final report 1986–1990. Natural Resources Institute for the European Community, Chatham, United Kingdom.

Hargrove, J. W. 1988. Tsetse: the limits to population growth. Med. Vet. Entomol. 2:203–217.

Hargrove, J. W. 1993. Target barriers for tsetse flies (*Glossina* spp.) (Diptera: Glossinidae): quick estimates of optimal target densities and barrier widths. Bull. Entomol. Res. 83:197–200.

Hargrove, J. W. and J. Brady. 1992. Activity rhythms of tsetse flies (*Glossina* spp.) (Diptera: Glossinidae) at low and high temperatures in nature. Bull. Entomol. Res. 82:321–326.

Hargrove, J. W. and M. J. Packer. 1993. Nutritional states of male tsetse flies (*Glossina* spp.) (Diptera: Glossinidae) caught in odour-baited traps and artificial refuges: models for feeding and digestion. Bull. Entomol. Res. 83:29–46.

Hargrove, J. W. and G. A. Vale. 1978. The effect of host odour concentration on catches of tsetse flies (Glossinidae) and other Diptera in the field. Bull. Entomol. Res. 68:607–612.

Harris, E. G., M. Brown and S. Smith. 1991. Laboratory investigations of insecticide impregnated materials for the control of New World screwworm fly. Final report to Joint FAO/IAEA Division. Natural Resources Institute for the European Community, Chatham, United Kingdom.

Jordan, A. M. 1986. Trypanosomiasis control and African rural development. Longman Group Ltd., Harlow, United Kingdom.

Mackley, J. W. and H. E. Brown. 1987. Efficacy of different-sized pellets of the screwworm (Diptera: Calliphoridae) adult suppression system during the wet and dry seasons in Mexico. J. Econ. Entomol. 80:629–635.

Maudlin, I., C. H. Green and F. Barlow. 1981. The potential for insecticide resistance in *Glossina* (Diptera: Glossinidae)—an investigation by computer simulation and chemical analysis. Bull. Entomol. Res. 71:691–702.

Mérot, P., J. B. Galey, H. Politzar, J. Filledier and A. Mitteault. 1986. Pouvoir attractif de l'odeur des hôtes nourriciers pour *Glossina* tachinoides en zone soudano-guineénce (Burkina Faso). Rev. Elev. Med. Vet. Pays Trop. 39:345–350.

Moorhouse, J. E., R. Yeadon, P. S. Beevor and B. F. Nesbitt. 1969. Method for use in studies of insect chemical communication. Nature (Lond.) 223:1174–1175.

Paynter, Q. and J. Brady. 1992. Flight behaviour of tsetse flies in thick bush (*Glossina pallidipes* (Diptera: Glossinidae)). Bull. Entomol. Res. 82:513–516.

Peterson, R. D. 1982. Influence of trap color and height above ground on capture of screwworms. Southwest. Entomol. 7:240–243.

Randolph, S. E. and D. R. Rogers. 1978. Feeding cycles and flight activity in field populations of tsetse (Diptera: Glossinidae). Bull. Entomol. Res. 68:655–671.

Snow, J. W., J. R. Coppedge, A. B. Broce, J. L. Goodenough and H. E. Brown. 1982. Swormlure: development and use in detection and suppression systems for adult screwworm (Diptera: Glossinidae) Bull. Entomol. Soc. Am. 28:277–284.

Takken, W. and D. L. Kline. 1989. Carbon dioxide and 1-octen-3-ol as mosquito attractants. J. Am. Mosq. Control Assoc. 5:311–316.

Torr, S. J. 1985. The susceptibility of *G. pallidipes* Austen (Diptera: Glossinidae) to insecticide deposits on targets. Bull. Entomol. Res. 75:451–458.

Torr, S. J. 1988a. The activation of resting tsetse flies (*Glossina*) in response to visual and olfactory stimuli in the field. Physiol. Entomol. 13:315–325.

Torr, S. J. 1988b. Behaviour of tsetse flies (*Glossina*) in host odour plumes in the field. Physiol. Entomol. 13:467–478.

Torr, S. J. 1988c. The flight and landing of tsetse (*Glossina*) in host odour plumes in the field. Physiol. Entomol. 13:453–465.

Torr, S. J. 1989. The host-oriented behaviour of tsetse flies (*Glossina*): the interaction of visual and olfactory stimuli. Physiol. Entomol. 14:325–340.

Torr, S. J. 1990. Dose responses of tsetse flies (*Glossina*) to carbon dioxide, acetone and octenol in the field. Physiol. Entomol. 15:93–103.

Torr, S. J. and M. J. R. Hall. 1992. Odour-baited targets to control New World screwworm, *Cochliomyia hominivorax* (Diptera: Calliphoridae): a preliminary study. Bull. Entomol. Res. 82:417–423.

Torr, S. J., M. T. P. Holloway and G. A. Vale. 1992. Improved persistence of insecticide deposits on targets for controlling *Glossina pallidipes* (Diptera: Glossinidae). Bull. Entomol. Res. 81:525–533.

Torr, S. J., A. G. Parker and G. Leigh-Browne. 1989. The responses of *G. pallidipes* Austen (Diptera:Glossinidae) to odour-baited traps and targets in Somalia. Bull. Entomol. Res. 79:99–108.

Vale, G. A. 1971. Artificial refuges for tsetse flies (*Glossina* spp.). Bull. Entomol. Res. 61:331–350.

Vale, G. A. 1974a. The responses of tsetse flies (Diptera: Glossinidae) to stationary hosts. Bull. Entomol. Res. 64:545–588.

Vale, G. A. 1974b. New field methods for studying the responses of tsetse flies (Diptera: Glossinidae) to hosts. Bull. Entomol. Res. 64:199–208.

Vale, G. A. 1977a. The flight of tsetse (Diptera: Glossinidae) to and from a stationary ox. Bull. Entomol. Res. 67:297–303.

Vale, G. A. 1977b. Feeding responses of tsetse flies (Diptera: Glossinidae) to stationary hosts. Bull. Entomol. Res. 67:635–649.

Vale, G. A. 1983a. The trap orientated behaviour of tsetse flies (Diptera: Glossinidae). Bull. Entomol. Res. 72:71–93.

Vale, G. A. 1983b. The effect of odours, wind direction and wind speed on the distribution of *Glossina* (Diptera: Glossinidae) and other insects near stationary targets. Bull. Entomol. Res. 73:53–64.

Vale, G. A. 1991. Responses of tsetse flies (Diptera: Glossinidae) to odour-baited trees. Bull. Entomol. Res. 81:323–331.

Vale, G. A. 1993a. Visual responses of tsetse flies (Diptera: Glossinidae) to odour-baited targets. Bull. Entomol. Res. 83:277–290.

Vale, G. A. 1993b. Development of baits for tsetse flies (Diptera: Glossinidae) in Zimbabwe. J. Med. Entomol. 30:831–842.

Vale, G. A. and D. R. Hall. 1985. The use of 1-octen-3-ol, acetone and carbon dioxide to improve baits for tsetse flies, *Glossina* spp. (Diptera: Glossinidae). Bull. Entomol. Res. 74:143–152.

Vale, G. A., S. Flint and D. R. Hall. 1986a. The field responses of tsetse flies, *Glossina* spp. (Diptera: Glossinidae) to odours of host residues. Bull. Entomol. Res. 76:685–693.

Vale, G. A., D. R. Hall and A. J. E. Gough. 1988a. The olfactory responses of tsetse flies, *Glossina* spp. (Diptera: Glossinidae) to phenols and urine in the field. Bull. Entomol. Res. 78:293–300.

Vale, G. A., J. W. Hargrove, G. F. Cockbill and R. J. Phelps. 1986b. Field trials of baits to control populations of *Glossina morsitans morsitans* Westwood and *G. pallidipes* Austen (Diptera: Glossinidae). Bull. Entomol. Res. 76:179–193.

Vale, G. A., D. F. Lovemore, S. Flint and G. F. Cockbill. 1988b. Odour-baited targets to control tsetse flies, *Glossina* spp. (Diptera: Glossinidae), in Zimbabwe. Bull. Entomol. Res. 78:31–49.

Warnes, M. L. 1990. The effect of host odour and carbon dioxide on the flight of tsetse flies (*Glossina* spp.) in the laboratory. J. Insect. Physiol. 36:607–611.

Warnes, M. L. and C. H. Green. 1992. Responses of female New World screwworm flies, *Cochliomyia hominivorax*, to swormlure-4 in the laboratory. Med. Vet. Entomol. 6:98–102.

WHO (World Health Organization). 1986. Epidemiology and control of African trypanosomiasis. Report of a WHO Expert Committee. W. H. O. Tech. Rep. Ser. 739.