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CONTROL OF TSETSE FLIES (DIPTERA: GLOSSINIDAE) WITH THE AID OF ATTRACTANTS

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ABSTRACT. A high degree of control of some *Glossina* spp. can be achieved by trapping. This is mainly because of their adenotrophic vivaparity, and consequently very low intrinsic rates of population increase. Calculations based on basic life table data have shown that it is only necessary to catch some 1–4% of the female population per day in order to achieve effective control. This is at least 8 times less than that required for *Anopheles albimanus.* Much attention has been given to the size and shape of traps. In general for the Palpalis Group of species, the vertically oriented biconical trap and its derivatives are highly effective, whereas for the Morsitans Group compact or horizontally oriented shapes are more attractive. Royal blue is highly attractive, and strongest landing responses are induced either on dark surfaces or those strongly reflective in the ultraviolet. Only carbon dioxide has been identified as an attractant for the Palpalis Group, but its use in traps is impractical. In contrast, a number of attractive compounds have been identified for the Morsitans Group, but there is much variation between species and within a species at various locations. A cocktail of all known attractants, except carbon dioxide, can increase trap captures of *Glossina pallidipes* by 15–20 times. Attractive substances in host breath include acetone, and in urine, 4-methyl phenol and 3-n-propyl phenol. The new generation of traps, or so-called targets, usually insecticide-impregnated that do not retain attracted flies, can be highly effective for controlling tsetse populations. However, the problem with tsetse control is primarily one of sustainability, in particular the problem of economically containing the threat of reinvasion of areas cleared of the fly.

INTRODUCTION

Tsetse flies (*Glossina* spp.) are virtually restricted to Africa south of the Sahara where they occur over some 11 million km^2. The 23 known species occupy habitats ranging from dry savannas, with sparse woody vegetation, to tropical rain forests. The genus is divided into 3 species groups on taxonomic grounds and, with some exceptions, the species within each group occur in the same general type of habitat. Thus, the 5 species of the Morsitans Group occur mainly in woodland savanna whereas most of the 13 species of the Fusca Group are forest species. The 5 species of the Palpalis Group also occur in forest vegetation but extend far from the blocks of rain forest, occupying strips of woodland along rivers, streams, and lakeshores far out into the African savannas.

Tsetse flies are the vector of human and animal trypanosomiasis. In the early years of the 20th century, many thousands of people died from sleeping sickness but today only some 25,000 new cases are reported each year (TDR 1990), although many others undoubtedly go undiagnosed and uncounted. In economic terms, the disease of domestic livestock is today of much greater economic importance than human trypanosomiasis. In cattle it causes loss of condition, anemia, abortions, and, if untreated, death. Perhaps more importantly, the presence of dense tsetse infestations can exclude cattle from extensive areas of potentially productive rangelands.

Tsetse control has long been one approach to the control of trypanosomiasis (Jordan 1986). Before the advent of modern insecticides, the clearing of vegetation, on which flies depend for their habitat, and the shooting of wild mammals, on which they primarily depend for their food, were widely practiced. The introduction of organochlorine insecticides in the late 1940s was followed by large-scale spraying campaigns in a number of countries. Many of these operations were successful and, because of highly selective application of insecticide, caused little contamination of the environment. Nevertheless, there were other problems, particularly cost, the logistical difficulties of mounting large-scale ground or aerial operations, and, increasingly, the realization that the operation had to be repeated regularly if disease control was to be maintained.

The time was appropriate for the reintroduction, and refinement, of a method of tsetse control that had been first employed in the early years of the 20th century.

THE CATCHING-OUT OF TSETSE POPULATIONS

Early campaigns against *Glossina palpalis* (of the Palpalis Group) in West Africa and *Glossina pallidipes* (of the Morsitans Group) in Zululand showed that a high degree of control could be achieved by trapping. The vulnerability of tsetse

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flies to trapping-out stems from their unusual life cycle, in particular their adenotrophic viviparity, which involves the ovulation of a single egg at a time and the retention of this egg within the uterus where it is fertilized and develops into a fully developed 3rd-instar larva. The first larva is not deposited until the female fly is about 18 days old, and thereafter a single larva is produced about every 10 days. Compared to most insects, tsetse flies have an extremely low intrinsic rate of population increase.

Calculations employing basic life-table data have shown that it is only necessary to remove some 1–4% of the female population per day to achieve an effective degree of control (Weidhaas and Haile 1978, Hargrove 1988). Even the cumbersome and unsophisticated traps used in the early tsetse control campaigns were capable, under the right circumstances, of achieving catches of this magnitude.

THE DEVELOPMENT OF ATTRACTANTS

The early work on trapping-out tsetse populations was not followed up until the 1970s. Initial emphasis was on overcoming the technical problems of designing lighter, easily portable traps; most of the developments were essentially of an *ad hoc* nature. Subsequently, advances in trap design and efficiency arose through a better understanding of tsetse behavior, in particular, in the present context, of fly responses to the visual stimuli presented by man-made devices (such as traps) and the realization that such devices could be made more attractive and effective by taking advantage of the olfactory sense of the fly.

Visual attractants: It has long been known that tsetse species have a well-developed sense of sight. An early observation was the attraction of some species to moving objects; this was quantified by Vale (1974b) who showed that about 16 times as many male *Glossina morsitans morsitans* and twice as many females, were caught on a mobile, compared to a stationary, bait. No difference was observed for female *G. pallidipes,* although males showed some response to movement. Laboratory studies on *G. m. morsitans* have shown that movement is a powerful activating stimulus and that responsiveness increases as starvation progresses (Brady 1972). In contrast, species of the Palpalis Group do not respond strongly to movement, although no comparable studies involving mobile and stationary baits have been undertaken.

Early traps were developed on a somewhat subjective basis; some, for example, were based on a perceived resemblance to a host animal. More recently, attention has been given to the shape and size of traps, with a view to maximizing catches. Vale (1974b) showed that a mobile bait was more attractive to *G. m. morsitans* if it had a compact shape than if it was a vertical rectangle. The preference of *G. m. morsitans* and *G. pallidipes* for compact shapes (squares, circles) compared to vertical rectangles was confirmed by Torr (1989), who presented them as stationary objects. These studies, and many others, of tsetse behavior were conducted in the absence of the confusing presence of man (who has a degree of visual and olfactory repellency to at least some *Glossina* spp.) with the aid of electric nets. An electric net consists of a grid of fine electrified wires 0.2 mm thick and 8 mm apart (Vale 1974a) and is virtually invisible to tsetse. Nets can be used in conjunction with mobile or stationary animals or with inanimate objects, and tsetse colliding with them are killed or stunned and then collected on sticky trays beneath the nets.

Fewer studies have been undertaken with species of the Palpalis Group; *G. p. palpalis* seems to respond less to size and shape than does *G. m. morsitans* and *G. pallidipes* but it is relatively more attracted to upright shapes (Laveissière et al. 1987). These findings are consistent with probable host location strategies—the vertically orientated biconical trap (Challier and Laveissière 1973) and its derivatives are highly effective for species of the Palpalis Group, which will feed readily on man, but less effective for the Morsitans Group, which are attracted more to compact or horizontally orientated shapes that approximate the shape of their usual bovid or suid hosts.

In early traps, for which hessian (sacking) was often used as the trap material, no attempt was made to exploit color as an attractant, despite numerous early reports that tsetse were more attracted to dark than light surfaces. It was not until Challier et al. (1977) found that substituting royal blue cloth for the white material originally used doubled the catch of *G. palpalis* in biconical traps that the potential of color began to be appreciated. Early versions of the present design of traps used in Zimbabwe were also predominantly white, with, like biconical traps, black entrances (Vale 1982). Substitution of royal blue in the Zimbabwe F_3 and other later traps increased the catch and blue traps performed better than white, gray, or black traps (Green and Flint 1986). Yellow traps caught fewer flies than any of this achromatic series, indicating that tsetse use true color information and not just intensity contrasts in trap-orientated behavior.

The analysis of observed color effects on behavior has been facilitated by using electric nets to distinguish between different aspects of tsetse behavior in relation to traps and surfaces of different colors. In the laboratory, color has been quantified in terms of spectrum reflectivity in different bands of the spectral visible to tsetse, which spans the near ultraviolet to near red (Green and Cosens 1983).

From field work in Zimbabwe with species of the Morsitans Group (Green 1986 and unpublished data, Torr 1989) and in Côte d'Ivoire with *G. p. palpalis* (Laveissière et al. 1987; Green 1988, 1989) it can be concluded that these economically important species respond to color in essentially the same manner. It is important to distinguish between effects on attraction and on landing responses. Attraction from a distance (to within about 0.5 m of an object) is controlled by spectral reflectivity in at least 3 different wavelength bands, blue, which increases the attractiveness of a surface, and ultraviolet and green–yellow, which diminish it. Dark surfaces are also attractive. Strongest landing responses occur on either dark surfaces or those strongly reflective in the ultraviolet (300–400 nm).

These results help to explain the apparent contradiction that, although black surfaces are as attractive as blue ones to many tsetse, black traps catch fewer flies than do blue ones (Green and Flint 1986). It is likely that the outer surfaces of a black trap encourage flies to land on the trap at the expense of trap entry responses. It is unclear why surfaces reflecting ultraviolet are unattractive from a distance and yet induce landing responses in nearby flies. It may be that ultraviolet reflectivity functionally represents skylight to a fly and hence is perceived as transparent and is neither attractive nor unattractive. Some support for this can be derived from laboratory studies that showed that tsetse can be strongly attracted to ultraviolet light, perhaps as an escape reaction towards what is perceived to be the sky in the unfamiliar circumstances of the laboratory (Green and Jordan 1983).

The royal blue material generally used in trap construction has a phthalogen pigment with high reflectivity (30–40%) at 460 nm (mid-blue), little ultraviolet reflectivity and relatively little green–yellow reflectivity—all indicated as being important for good trap performance. If other shades of blue are substituted in traps, catches are lower (Gouteux et al. 1981, Green 1988).

Olfactory attractants: Although it has been known for many years that catches of some *Glossina* spp. can be increased if animals or some animal products are associated with a trap, it is only relatively recently that the true importance of olfaction has been determined. Much of the early work was poorly controlled and often flawed by the presence of a human observer. A significant breakthrough was made when Vale (1974b) evaluated the role of the odor of potential hosts in attracting tsetse flies in the absence of any visual element of the hosts and of any visual or olfactory stimuli of a human observer. By constructing an underground pit, putting an ox in the pit, and venting the odors from the pit into the vicinity of an electric net, the catches on the net of male *G. m. morsitans* and *G. pallidipes* were increased by some 10 times and those of females by nearly 20 times. Increasing the number of oxen in the pit progressively increased the catch (Vale and Hargrove 1975, Hargrove and Vale 1978). Refinements of the technique showed that most of the attraction could be accounted for by odors produced at the head of an ox. Subsequently, carbon dioxide, 4 ketones, and 2 aldehydes, of which acetone was the cheapest and most effective (Vale 1980), and 1-octen-3-ol (octenol) (Hall et al. 1984) were identified as attractants in ox breath. Butanone can be substituted for acetone, and at lower doses (Vale and Hall 1985a).

The combination of carbon dioxide, acetone, and octenol increased catches by up to 60 times at high enough doses but this is, to some extent, academic as, although carbon dioxide can be used to improve the efficiency of sampling, it is impractical to employ this gas with traps in a large area catching-out control operation. In the absence of carbon dioxide, acetone and octenol increased the catch of *G. pallidipes* some 3–5 times and of *G. m. morsitans* about 2–3 times; at high doses, the dose–response course showed a plateau for acetone, and a decline for octenol (Vale and Hall 1985b).

Buffalo urine (Owaga 1984) and ox urine (Vale et al. 1986a) are also attractive to tsetse, particularly *G. pallidipes*; the active components are in the phenolic fraction (Hassanali et al. 1986), with 4-methyl phenol and 3-n-propyl phenol accounting for most, if not all, of the attractiveness of urine (Bursell et al. 1988). When combined with acetone and octenol, these 2 phenols increased the catches of *G. pallidipes* by some 15–20 times and of *G. m. morsitans* by some 3–4.5 times. The responsiveness of *G. pallidipes* to this combination of attractants is not the same throughout its range; in Somalia, for example, trap catches were only increased by about 4 times (Torr et al. 1989).

Of the *Glossina* spp. investigated so far, none is as attracted to the known olfactory attractants as *G. pallidipes*. The other 2 subspecies of *G. morsitans* (*G. m. submorsitans* and *G. m. centralis*) are attracted to about the same degree as *G. m. morsitans* (PAN 1989, Slingenbergh 1992). Species of the Palpalis Group show little or no response to any of the known attractants, other than carbon dioxide. *Glossina tachinoides* is more responsive than the other species but trap catches have been increased, at best, by only 2.5 times (Filledier and Mérot 1989). Most species of the Fusca Group, which are of relatively minor economic importance, have not been investigated; *G. longipennis* is attracted strongly by acetone, octenol, and 4-methyl phenol (Kyorku et al. 1990).

Comparisons of synthetic and natural ox odor indicate that the former results in catches only half those obtained with natural odor, suggesting that some attractants remain to be identified. These may be highly volatile substances, as, despite much effort, they have not so far been isolated.

SOME TSETSE CONTROL OPERATIONS EMPLOYING ATTRACTANTS

Visual and olfactory attractants for *Glossina* spp. have been incorporated in several control trials and operations and have been employed in a variety of ways. They can be used simply to improve the performance of a trap, with no involvement of insecticide, but more usually they are associated with a trap or other device that is treated with a lethal insecticide. All these approaches are now referred to as bait systems of control.

Insecticide-treated livestock: Throughout the search for olfactory attractants, the ideal against which they have been measured has been the natural odor of cattle. A logical extension of this is to employ cattle themselves as the attractive bait and to make the animals lethal to tsetse by treating their hides with insecticide. This is not a new idea, early attempts to treat animals with DDT were abandoned because too-frequent treatment was required and the cost was unacceptable. The development of long-lasting formulations of synthetic pyrethroid insecticides, which can be applied to cattle by dipping or by "pour-on", has been followed by a number of field trials. In Zimbabwe effective control of trypanosomiasis was achieved over some 2,500 km^2 (Thomson and Wilson 1992). Other successful trials have been reported in Kenya (Löhr et al. 1991) and Burkina Faso (Bauer et al. 1992).

The technique has great promise, particularly in areas where keeping cattle is important and where there are few other potential hosts for tsetse, but it does not have universal applicability. Further discussion is consequently restricted to control operations employing artificial, rather than natural, baits.

Traps without insecticide: Although early attempts to catch-out tsetse populations by trapping did not involve any insecticide, once first-generation organochlorine insecticides became available, a number of small-scale trials were undertaken in which the effectiveness of the traps was enhanced by impregnating them with such chemicals. This also occurred later, after the development of the biconical trap in West Africa, when a number of trials with the traps impregnated with insecticide, generally deltamethrin, demonstrated its effectiveness as a means of controlling species of the Palpalis Group (Laveissière and Couret 1980).

More recently, some workers have advocated a return to the use of traps without the addition of insecticide. They are considered to be especially appropriate where local communities are expected to make, locate, and maintain their own traps. They have the advantage that any flies caught are retained and thus act as a guide to the amateur of the progress of the control measures. Pyramidal traps (a derivative of the biconical) have been used to control *G. fuscipes quanzensis* in the Republic of Congo (Gouteux and Sinda 1990). This species is a member of the Palpalis Group and no olfactory attractants were employed, with success being attributable solely to the visual appearance of the traps.

In Kenya, an attempt has been made to control *G. pallidipes*—a much more mobile species than those of the Palpalis Group—on 2 group ranches where the local Maasai cattle owners were actively involved (Otieno and Dransfield 1990). A cheap and simple trap was developed and evaluated (Brightwell et al. 1987); the trap was made more effective by cheap olfactory attractants, substituting cattle urine for the synthetic phenols. A tsetse control campaign demonstrated the effectiveness of the technology, but the long-term objective of tsetse control being managed and funded solely by the local community has yet to be achieved.

Insecticide-impregnated targets: If, as has usually recently been the case, a trap is to be impregnated with insecticide to assist the catching-out of a tsetse population, would it not be more appropriate to employ a simpler and cheaper device with no means of retaining captured flies? Only brief contact with insecticide-treated material is required to kill a fly (Torr 1985). Consideration of this question led to work in a number of countries that showed that simple insecticide-impregnated targets can, with no loss of efficiency, be substituted for a similarly treated trap. These are described as "écrans" in the French literature and as "screens" or "targets" in the English. The English word "target" is used here to describe all such devices. Electric nets have made a major contribution to target design;

targets alone cannot be evaluated as they retain none of the flies that they kill.

A number of campaigns in West Africa have demonstrated the efficacy of simple blue cloth targets (120 × 90 cm), each impregnated with 100 mg active ingredient of deltamethrin, for controlling populations of *G. tachinoides* and *G. palpalis* occupying linear habitats. Laveissière and Couret (1981) located 876 such targets along 79 km of river and achieved 98% reduction of fly populations within a few days. Such rapid rates of population reduction are typical of a number of campaigns conducted in linear habitats where the threat of reinvasion is minimal. In more humid regions, control of the Palpalis Group, no longer restricted to linear habitats, is more difficult, but even here simple targets can achieve population reductions in the region of 90% (Laveissière et al. 1986). Odor attractants are inappropriate and have not been employed.

The control of species of the Morsitans Group in the vast savanna regions of Africa is a much greater problem, particularly as these species are highly mobile. Even at high placement density, baits relying on visual attraction only can have doubtful efficacy (Schoenefeld 1983); it was the development of odor attractants that provided the required increase in efficiency. Most of the development work and early field trials were undertaken in Zimbabwe, where it is now standard practice to pour acetone (or butanone) in a bottle and to bury it in the ground close to the target and with the neck exposed, and to fit into a pocket on the target a sealed polythene sachet containing 4-methyl phenol, octenol, and 3-n-propyl phenol (in the ratio 8:4:1) through which the odors diffuse. A slow, controlled rate of release of attractants can be achieved for more than a year (Hall et al. 1992). This, combined with an effective life of the insecticide on the target of more than 15 months, means that servicing of targets can be infrequent.

The first Zimbabwe trial was on an island in Lake Kariba; tsetse were eradicated using insecticide-impregnated targets, baited with acetone and octenol (Vale et al. 1986b). Since then larger successful trials were conducted and by the early 1990s targets had become the method of choice for routine tsetse control operations in Zimbabwe. By 1993, some 60,000 targets were deployed in the country (V. Chadenga, unpublished data).

Experiments have been undertaken to determine optimal target density. There is a relationship between density and the speed of fly population decline, but this can be obscured by a variety of factors (Pollock 1991). Actual target densities used therefore vary but in Zimbabwe it is usual to employ some 1–2 km^{-2} for *G. pallidipes* and 4–6 km^{-2} for *G. m. morsitans* (Sherení 1990), reflecting the greater efficiency of baits for the former species.

The target technique developed in Zimbabwe has been evaluated in a number of other countries and it appears that, when correctly applied, good control of species of the Morsitans Group can be achieve at target densities of only a few per square kilometer.

CONCLUSIONS

The exploitation of the highly efficient host location behavior of the adult tsetse fly in order to attract them to lethal artificial baits has been a major technical achievement, involving electrophysiologists, chemists, and behaviorists in the laboratory in support of workers in the field. The identification and exploitation of odor attractants is probably the best example of the use of kairomones to control any vector of human or animal disease. However, this statement must be qualified, as the currently known range of odor attractants makes no contribution to the control of the important Palpalis Group.

In comparison with other modern methods of tsetse control, bait techniques use much less insecticide (or even none at all) per unit area; it is generally agreed that they present no risk of environmental contamination. This, together with their relative simplicity, has made them popular with both governments and donors. However, the cost of making a trap or target is only a fraction of the overall cost of placing it in the field and maintaining it there for the required period of time—which may be indefinitely. A number of comparisons of relative costs of bait techniques and other methods of tsetse control have been made and there is much variability in the results, depending on such factors as target density, frequency of servicing, duration of control, and type of terrain (Brandl 1988, Barrett 1991). Often a bait technique can be the cheapest option.

It has been repeatedly demonstrated over the years that, because of their specialized reproductive strategy and high susceptibility to insecticides, it is relatively easy to kill tsetse flies and to significantly suppress tsetse populations. The exploitation of visual and olfactory attractants is just the latest of a number of techniques by which this can be achieved. These latter methods have many advantages but appreciation of these should not obscure the fact that the main problem with tsetse control—common to whatever method is employed—is that of sustainability.

The economic justification of some methods of tsetse control, such as the spraying of insecticide from the ground or from the air, is that they offered prospects of tsetse eradication over a prescribed area and hence a one-off cost. However, this can be achieved only under very special circumstances and examples of successful operations are very few (Jordan 1986). There is now increasing recognition that most future control campaigns will involve continuing population suppression, and that costs will be recurrent (Dransfield et al. 1991). The main problem is that of economically containing the threat of reinvasion of areas where population suppression, or even removal, has been achieved. The flexibility of bait techniques offers hope for the future. Some consider that community participation in tsetse control may be the solution but this approach—over more than an initial period of enthusiasm—is as yet unproven.

The technical elegance and feasibility of tsetse control techniques involving visual and olfactory attractants are not in doubt. To what extent they can be economically exploited to solve the problem of sustainability of tsetse control remains to be determined.

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