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Development of odour-baited traps for *Glossina swynnertoni* (Diptera: Glossinidae)

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Abstract

Three new prototype traps, (S1–S3), were developed during studies of the behavioural ecology of *Glossina swynnertoni* Austen in Kenya and Tanzania. The traps were compared in latin square experiments relative to the regular biconical trap as a standard and a selection of other conventional tsetse traps. Observations were also made on fly behaviour in the vicinity of traps using electric nets and sticky materials. When baited with acetone and 1-octen-3-ol, the S1 trap was 3.5 times as effective in catching *G. swynnertoni* in Kenya as the biconical trap. In Tanzania, the relative performance of the S1 and biconical traps differed; also, both traps were found to be inferior to an all-black, sticky 1-m^2 target. A second prototype (S2) performed slightly better than the biconical trap, but was still inferior to the black target. The final prototype (S3) was 2.9 times as effective as the biconical trap and performed as well as the black target. The potential for further improvement of traps for capturing *G. swynnertoni* and flies of the *G. morsitans* Westwood group is discussed.

Introduction

The *morsitans* group of tsetse flies (*Glossina* spp. (Diptera: Glossinidae)) are important vectors of animal trypanosomiasis in the productive savannahs of Africa where large numbers of pastoralists graze their livestock. In the past decade, considerable advances have been made in the sampling and control of savannah tsetse through the use of artificial bait technology. This technology combines a visually attractive killing device, e.g. a mechanical trap or an insecticide-impregnated cloth target, with olfactory attractants that together mimic a natural host (Vale, 1993; Green, 1994).

In the sole case of *G. pallidipes* Austen (Diptera: Glossinidae), effective traps have been developed (Brightwell *et al.*, 1991) and are being deployed on a large scale with success (Brightwell *et al.*, 1997). For other savannah tsetse, including *G. swynnertoni* Austen, there are no truly effective traps; hence, control has relied on the use of insecticide-impregnated targets or, more recently, live baits (Green, 1994). Blue / black or all-black targets, with or without flanking panels of netting, have been used to control *G. m. submorsitans* Newstead (Filledier & Politzar, 1985; Mérot & Filledier, 1985; Leak, 1996), *G. m. centralis* Machado (Willemse, 1991; Knols *et al.*, 1993), *G. m. morsitans* Westwood (Vale *et al.*, 1988; Vale, 1993) and *G. swynnertoni* (TPRI, 1994) in both pilot trials and large-scale operations.

Aside from the problem of control, detection and monitoring of members of the *morsitans* group, particularly at low population density, has been constrained by the lack of effective traps. The main problem compounding trap development has been the tendency of *morsitans* tsetse to circle rather than alight on artificial objects (Hargrove, 1976, 1980a; Green, 1993). The stimuli presented by artificial objects are still far from ideal, with considerable room for improvement. A typical example is *G. m. morsitans* which rarely lands on artificial stationary objects (and hence enters traps) in the absence of appropriate host odour cues, particularly carbon dioxide (Vale & Hall, 1985a,b).

Studies on *G. m. morsitans* have provided most of the information available on both close- and long-range, trap-orientated behaviour of flies in the *morsitans* complex (Green, 1993). These studies have shown that careful manipulation of size, shape and colour can enhance the visual attractiveness of artificial objects, as well as landing behaviour (Hargrove, 1980a; Vale, 1982; Green, 1986; Green

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& Flint, 1986). However, it has been difficult to enhance trap entry, and hence, the focus of attractive bait technology has remained largely on the refinement of targets (Vale, 1994).

The particular difficulty of trapping *Glossina swynnertoni* has been known for over 60 years (Lloyd, 1935). *G. swynnertoni* is nominally a separate species, but it is both ecologically and genetically similar to the subspecies of *G. morsitans* (Gooding, 1997). Other than the early trials of some simple traps that proved inefficient (Swynnerton, 1933), there have been no concerted efforts to develop an efficient trap and bait system for *G. swynnertoni* (Brightwell & Dransfield, 1997).

Here, we report the development and refinement of a practical cloth trap (the S3) for this species. The objective was to develop a simple mechanical device equal in efficiency to a typical, black 1-m^2 target. The development of the S3 now provides a convenient monitoring tool and opens up the possibility of control with traps as an alternative to the use of insecticide-impregnated targets.

Materials and methods

The study was carried out at Naitolya in northern Tanzania (36° 03' E, 03° 40' S). This work followed experiments on trap development (Ndegwa, 1997) at Aitong, Maasai Mara in southwestern Kenya (35° 10'E, 1°10'S); one of these experiments is reported here. The two areas are within a discontinuous *G. swynnertoni* belt (Stiles *et al.*, 1994) that stretches astride the Kenya–Tanzania border in an area inhabited by nomadic or semi-nomadic Maasai. The vegetation in both areas consisted of relatively open *Acacia*–*Commiphora* woodland.

Standard trap and odour baits

The biconical trap with a lower royal blue cone, a white mosquito netting upper cone and black interior targets (Challier *et al.*, 1977) was adopted as a standard trap. It has been used for sampling *G. swynnertoni* in Tanzania for many years (TPRI, 1994), although it is probably not an optimal trap for this species (Ndegwa, 1997). In all experiments, traps or targets were baited with acetone and 1-octen-3-ol. These baits are used as attractants for the closely related *G. m. centralis* (Willemse, 1991) and *G. m. submorsitans* (Politzar & Mérot, 1984) and are components of the baits used for *G. m. morsitans* in Zimbabwe (Vale, 1993). They also increase catches of *G. swynnertoni* in Tanzania (TPRI, 1994). Acetone was dispensed from 100-ml plastic bottles with a 2-cm diameter opening (*c.* 500 mg h^{-1}); 1-octen-3-ol was dispensed from 50-ml glass bottles with a 0.2-cm diameter hole in the lid (*c.* 0.4 mg h^{-1}). Both dispensers were dug into the ground 30 cm behind traps (upwind) and sheltered from rain.

Descriptions of experimental traps

The S1 trap (fig. 1a) was developed during preliminary experiments in Kenya (Ndegwa, 1997). It has an upper triangular white netting cone covering a central triangular bodice of three turquoise blue panels (90 × 50 cm) joined end to end to form a triangle. The interior of the trap consists of three black panels joined on one end to form a three-vaned design. The outer edges of each vane are attached to the inner corners of the blue triangle and extend both up into the cone and down into the lower part of the trap as an open hanging triangular-shaped target.

The S2 trap (fig. 1b) is a complex modification of the S1 trap. The turquoise blue sides are 90 × 90 cm with three central entrances (40 × 40 cm), one on each side, and 8 cm above the bottom. A white netting bottom is also added to the trap. The interior consists of a target of three black panels (58 × 25 cm) joined together on the longer axis into a three-vaned design visible from the outside through each of the entrances. This target is attached to the inner corners of the blue triangle above a dull white cotton cloth (58 × 25 cm). The white panels are similarly designed and join the lower edges of the target, touching the bottom white netting. The cone is attached to the inside of the blue triangle, as in the M3 trap (Mhindurwa, 1994), with the black cloth extending into the cone like the S1 trap. The S3 trap (fig. 1c) is a refinement of the S2 trap, with only the turquoise blue panels changed to royal blue, 'wings' (90 × 30 cm) added, and the surface above each entrance slanted outwards at an angle of 45°.

Comparisons to conventional traps

Two preliminary multiple-comparison experiments were conducted with a selection of traps for tsetse to guide design modifications. The first experiment was conducted in Kenya; others were carried out in Tanzania. In experiment 1, S1, biconical, NG2G (Brightwell *et al.*, 1991), Vavoua (Laveissière & Grébaut, 1990) and Siamese (Kyorku *et al.*, 1995) traps were compared in a 5 × 5 latin square, replicated three times with sites and days as row and column effects. The experiment was set in a homogeneous *Acacia* woodland with traps spaced at 200-m intervals.

In experiment 2 (4 × 4, three replicates), the S1 trap was compared with the biconical and the Nzi trap (a generic blue cloth / black cloth / white netting winged-triangular trap highly efficient at capturing many Diptera (Mihok, unpublished). We also adopted a new standard to address our overall objective: a black 1 × 1 m all-cloth target (Willemse, 1991; Vale, 1993) covered with panels of clear plastic sticky fly rolls (Fly Control Adhesive Film, Rentokil Stock No. FE 22 / G; supplied by Agrisense, UK). Sticky fly rolls are transparent plastic sheets in roll form coated with a 30-cm wide colourless, odourless sticky material on one surface. The combination of the plastic base with the chemical adhesive transmits 85–90% of light at wavelengths above 400 nm. The adhesive itself absorbs strongly in the ultraviolet, resulting in diminished transmittance below 400 nm (30% at 370 nm, Mihok, personal communication).

Following experiment 2, the S1 trap was modified to produce the S2 trap based on the following observations: (i) many flies that landed on the black target were not being caught; (ii) many flies flew under the trap; and (iii) transfer into and upward movement within the cone was sub-optimal. The S2 prototype was then compared with the biconical, S1 and Nzi traps and the black sticky target in a 5 × 5 latin square replicated three times as experiment 3. In experiment 4, a final winged prototype (S3) was tested against the biconical and S2 traps and the sticky target in a 4 × 4 latin square design replicated three times.

Data from each experiment were subjected to a $\log_{10}$ (n+1) transformation prior to Analysis of Variance. Each sex was analysed independently as there are numerous differences in the behaviour of the sexes in this species

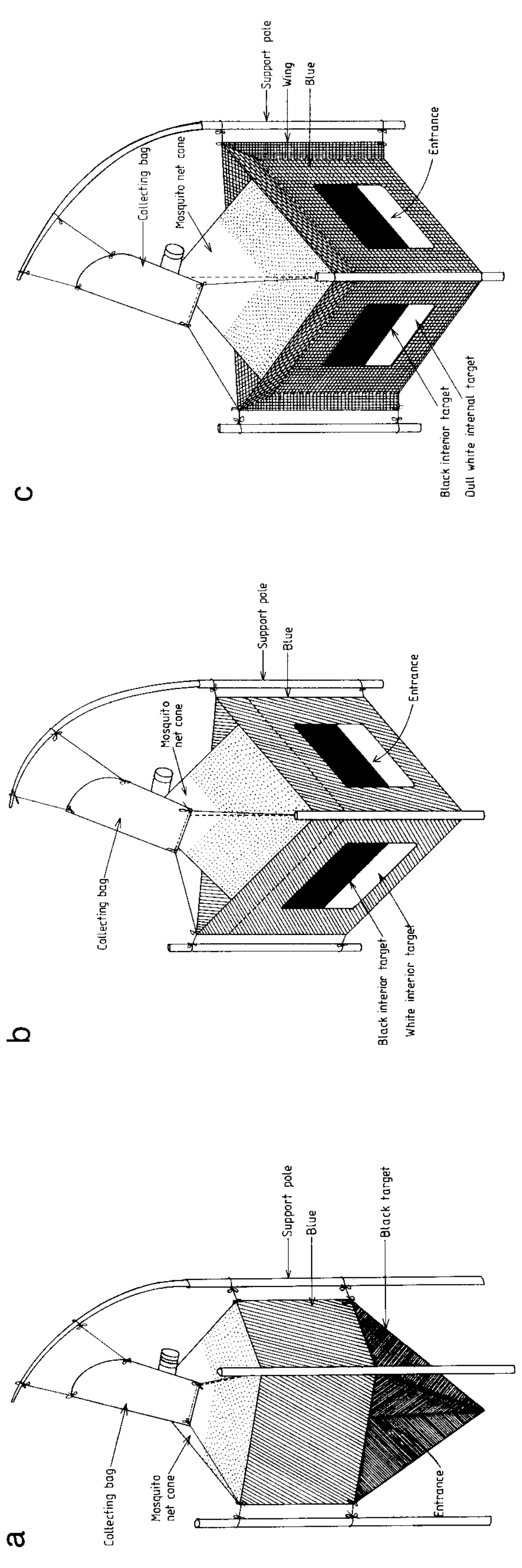

Fig. 1. Schematic drawings of (a) S1 trap: the blue panel on each side is 90 cm wide and 50 cm high; (b) S2 trap: each side panel is 90 × 90 cm; and (c) S3 trap: each side panel is 90 × 90 cm.

(Ndegwa, 1997). If the treatment effect was significant, means were compared using the Student-Neuman-Keul's (SNK) test. Means are presented as detransformed data. Significance was judged at the 0.05 level of probability.

Estimation of trap and target efficiency

The capture efficiencies of the Nzi and S2 traps, and the black sticky target were measured to help differentiate attractiveness from efficiency using an incomplete ring of electric nets. Two sites were used for each comparison with treatments crossed-over between days over a total of four days for the S2 trap, and two days for the Nzi trap and the sticky target. The traps (or target) were surrounded by three equally-spaced electrified nets (1 × 1 m) at a radius of 3 m covering 14.8% of the perimeter. Flies were collected from water-filled trays hourly between 11.00 am and 4.00 pm, spanning the peak activity period. Efficiency was calculated from the inside net catches only (Hargrove, 1980b). It represents the percentage of flies captured relative to an estimate of the number of flies approaching the object based on various assumptions about how flies behave relative to the incomplete ring of electric nets.

Observations on behaviour in relation to trap investigation

To guide the development of a final prototype trap, we conducted a series of trials to obtain quantitative observations of three features of fly behaviour around the S2 prototype. These were: circling or flight around the trap; landing or alighting on the outside surfaces of the trap; entry into the trap and retention in the collecting non-return cage / bag.

Circling or flight around the trap

The S2 trap was surrounded by radial electrified nets (1 × 1 m) placed at 0–1 m; 1–2 m and 2–3 m from each of the outside corners (fig. 2). A control trap, without electrified nets, was set up at a matching site. The electrified nets were rotated every day with respect to distance from each of the three corners of the trap and the orientation (NW–E–SW). The traps were crossed-over on the third day. The trial was run from 10.00 am to 4.00 pm for six days.

Landing or alighting on the outside surfaces of the trap

The S2 trap was set and covered with panels of sticky fly rolls on all surfaces except for the white netting cone and the bottom. A control trap was set at a matching site and was covered with the same plastic panels, but without the adhesive. The trial was run for six days with a cross-over between sites on the third day.

Entry into the trap and retention in the cone/cage

Each of the three entrances of the S2 trap was covered with a panel (42 × 42 cm) of sticky fly roll positioned between the entrance and the inner black target at about 4 cm from the entrance. For the control trap, a plastic panel without adhesive was attached to the inside of the trap. Both traps were operated for six days with a cross-over between sites on day three.

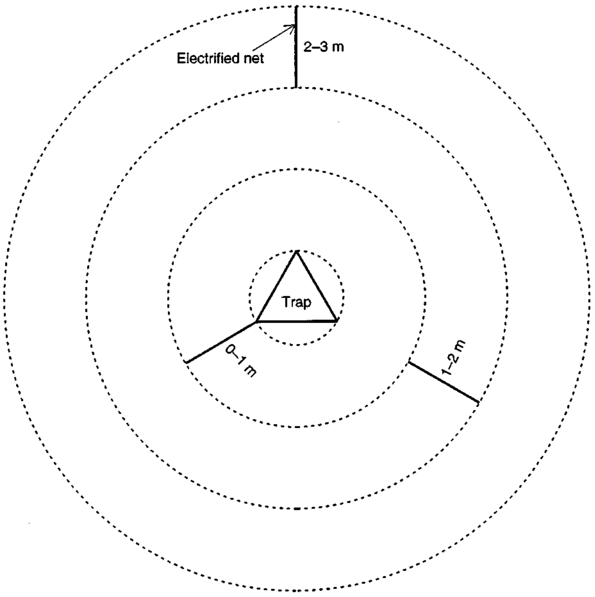

Fig. 2. Arrangement of the radial electrified nets used to investigate fly circling behaviour around the S2 trap.

Results

In experiment 1 in Kenya (table 1), both male and female catches differed significantly among traps. The S1 trap performed best, catching 3.2 and 3.5 times as many males and females, respectively, as the biconical trap. The Siamese trap caught significantly more males than the biconical trap, but was significantly inferior to the S1 trap for both sexes. Catches in Vavoua and NG2G traps were similar to, or lower than, those in the biconical trap. In experiment 2 in Tanzania (table 2), fly densities were rather low and we detected no significant differences in catch between traps. However, all traps were significantly inferior to the black sticky target. Overall, the target caught three times as many flies as the biconical trap. When the S2 trap was included in experiment 3 at much higher fly density, both male and female catches differed significantly among traps (table 3). The S2 trap caught 1.5 times as many flies as the biconical trap, but fewer than the target.

The good daily catches obtained in the simple Nzi trap and the more complex S2 trap prompted further work to differentiate attractiveness from efficiency relative to the target (table 4). Although catches were low in these trials with incomplete rings of electric nets, the S2 trap and the black sticky target clearly had similar, and moderately good efficiencies (31% and 27%, respectively), despite lower catches in the S2. In contrast, lower catches in the Nzi trap were related to lower capture efficiencies, particularly for males.

To understand the reasons for the above trap and target differences, we next quantified three behaviours around the S2 trap by intercepting flies in various ways, and comparing the effects on catch relative to a control trap. In the first trial with radial electric nets, of 637 flies that were in the vicinity of the trap, many (431 or 68%) flew around it, with the majority (383 or 89%) circling very close (0–1 m). For all

Table 1. Backtransformed mean catches per trap per day and capture indices relative to the biconical trap for *Glossina swynnertoni* in experiment 1, comparing the S1 trap with other tsetse traps at Aitong, Kenya during July 1996.

	Males		Females	
Trap	Mean	Index	Mean*	Index
Biconical	4.4^{a} (0.64±0.02)	1.0	5.3^{a} (0.72±0.11)	1.0
Vavoua	2.3^{b} (0.36±0.09)	0.5	3.8^{b} (0.58±0.06)	0.7
NG2G	2.4^{b} (0.38±0.14)	0.5	6.3^{a} (0.80±0.10)	1.2
Siamese	9.0^{c} (0.95±0.12)	2.0	7.7^{a} (0.89±0.05)	1.5
S1	14.0^{d} (1.15±0.08)	3.2	18.4^{c} (1.26±0.13)	3.5
	F-ratio=6.5*		*F*-ratio=10.2*	

Means in the same column followed by different letters are significantly different (SNK test); Index, ratio of detransformed treatment mean to detransformed mean of biconical trap; *F*, ANOVA statistic for the effect of trap type treatments, *significant $P<0.05$. Numbers in parentheses show transformed means ± standard error.

Table 2. Backtransformed mean catches per trap per day and capture indices relative to the biconical trap for *Glossina swynnertoni* in experiment 2 comparing the S1 trap with other traps at Naitolya, Tanzania during August 1997.

Trap type	Males	Index	Females	Index
Target	17.4^{a} (1.24±0.10)	3.0	18.2^{a} (1.26±0.13)	2.6
S1	6.5^{b} (0.81±0.10)	1.1	9.8^{b} (0.99±0.11)	1.3
Nzi	6.1^{b} (0.78±0.11)	1.1	7.1^{b} (0.81±0.12)	1.0
Biconical	5.8^{b} (0.77±0.12)	1.0	6.5^{b} (0.85±0.16)	0.9
	F-ratio=11.9*		*F*-ratio=6.6*	

Means in the same column followed by different letters are significantly different (SNK test); Index, ratio of detransformed treatment mean to detransformed mean of biconical trap; *F*, ANOVA statistic for the effect of trap type treatments; *significant ($P<0.05$). Numbers in parentheses show transformed means ± standard error.

Table 3. Backtransformed mean catches per trap per day and capture indices for *Glossina swynnertoni* at Naitolya, Tanzania comparing the S1 trap with other traps in experiment 3.

Trap type	Males	Index	Females	Index
Target	42.9^{a} (1.63±0.05)	2.3	74.4^{a} (2.08±0.05)	1.9
S2	24.2^{b} (1.38±0.05)	1.3	62.0^{ab} (1.94±0.04)	1.6
S1	21.5^{b} (1.33±0.05)	1.2	49.7^{bc} (1.85±0.04)	1.3
Biconical	18.6^{b} (1.27±0.04)	1.0	38.6^{c} (1.76±0.05)	1.0
Nzi	18.2^{b} (1.26±0.06)	1.0	41.9^{c} (1.78±0.05)	1.1
	F-ratio=7.8**		*F*-ratio=11.0**	

Means in the same column followed by different letters are significantly different (SNK test); Index, ratio of detransformed treatment mean to detransformed mean of biconical trap; *F*, ANOVA statistic for the effect of trap type treatments; *significant ($P<0.05$). Numbers in parentheses show transformed means ± standard error.

circling flies (383 + 31 + 17), the drop in catch relative to the control suggested that few (19%) would have been captured (287 − 206 of 431, table 5), had they not been electrocuted. In the second trial, with the trap covered with sticky materials, most of the approaching flies (546) appeared to land without entering directly (459, table 6). Similarly, the drop in catch relative to the control suggested that few (19%) would have been captured (174 − 87 of 459), had they not been intercepted on the sticky panels. Comparing absolute numbers from these two ways of enumerating flies that largely evade capture, it seems likely that many, but not all of the flies which circled the trap also landed on the outside surfaces.

In the third trial, which enumerated trap entry and escape from the inner structures, of the flies that passed through the entrances into the main body of the trap (table 7), 77% were intercepted by the sticky material on the inner target, whereas 24% bypassed the target, moved upwards and were retained in the collecting bag. For these entering flies, the drop in catch relative to the control suggests that 61% moved into the cone and were eventually caught (205 − 69 of 224, table 7), whereas 39% escaped.

Based on the above semi-quantitative observations, the S2 trap was modified to address various deficiencies. Since the interior design permitted only moderate levels of escape, it was retained. Three ‘wings’ were added to each corner of the triangle to intercept circling and landing flies. Similarly, the panel above each entrance was slanted outwards to direct landing flies towards the entrances. Lastly, the turquoise blue colour was changed to royal blue as other experiments indicated that there was no advantage to this feature.

The results of experiment 4 testing the final prototype (S3), against the S2 and biconical traps, and the black sticky target, are shown in table 8. The S3 trap performed significantly better than the biconical trap, with a 2.4- and 3.2-fold significant increase for males and females, respectively. Catches in the S3 trap were the highest of all three traps, and were not statistically different from those obtained with the black sticky target.

Table 4. Estimated capture efficiencies of S2 and Nzi traps, and the black sticky target for *Glossina swynnertoni*.

Trap	Sex	Total number of flies caught			Efficiency* (%)
		Trap	Inside net	Outside net	
S2	Males	68	27	22	27
	Females	120	36	49	33
	Total	188	63	71	31
Target	Males	41	17	13	26
	Females	55	12	28	28
	Total	96	38	41	27
Nzi	Males	4	16	4	4
	Females	35	26	24	17
	Total	39	42	28	12

* Capture efficiency (E) was calculated from the inside net catches using the formula $E = x / [x + (y/P)]$, where x is the trap catch; y, the inside net catch and P, the proportion of the perimeter covered by the nets (Hargrove, 1980b).

Table 5. Total catches of *Glossina swynnertoni* in and around an S2 trap surrounded by radial electrified nets compared with a control trap.

	Males	Females	Total	Flies intercepted by nets (%)
Electrified net catches:				
0–1 m	102	281	383	89
1–2 m	14	17	31	7
2–3 m	5	12	17	4
Total on nets	121	310	431	
Trap catch	64	142	206	
Total: nets+trap	185	452	637	
Control trap catch	82	205	287	

Table 6. Catches of *Glossina swynnertoni* in and on an S2 trap covered with panels of sticky fly rolls on the outside surfaces.

	Males	Females	Total
Catch on sticky panels	174	285	459
Trap cage catch	26	61	87
Trap catch+sticky panels	180	346	546
Control trap catch	33	141	174

Table 7. Catches of *Glossina swynnertoni* on sticky panels on the inside of the entrances of the S2 trap.

	Males	Females	Total	Proportion of flies caught (%)
Entrance panels	94	130	224	77
Trap cage catch	22	47	69	24
Total	116	177	293	
Control trap catch	78	127	205	

Table 8. Backtransformed mean catches and capture indices for *Glossina swynnertoni* comparing the S3 trap with other traps at Naitolya in Tanzania in experiment 4.

Trap type	Males	Index	Females	Index
Target	20.9^{a} (1.32±0.10)	2.9	30.8^{a} (1.49±0.11)	2.4
S3	17.7^{a} (1.25±0.12)	2.4	41.5^{a} (1.62±0.10)	3.2
S2	10.5^{b} (1.02±0.11)	1.5	25.1^{b} (1.40±0.09)	2.0
Biconical	7.2^{c} (0.86±0.12) F-ratio=16.4*	1.0	12.8^{c} (1.11±0.10) F-ratio=8.3*	1.0

Means in the same column followed by different letters are significantly different (SNK test); Index, ratio of backtransformed treatment mean to backtransformed mean of biconical trap; F, ANOVA statistic for the effect of trap type treatments; *significant (P<0.05). Numbers in parentheses show transformed means ± standard error.

Discussion

Glossina swynnertoni has remained a relatively unstudied species since the pioneering work of Swynnerton 60 years ago. Thus, no practical trap exists for this important vector of human and animal trypanosomiasis in East Africa (Brightwell *et al.,* 1997). Researchers have simply relied on techniques such as fly rounds or vehicle patrols to obtain semi-quantitative information on this fly's distribution and abundance (Moloo *et al.,* 1971, 1973). Here, we have shown that one can catch *G. swynnertoni* in a practical cloth trap such as the S3 with an efficiency equal to a typical black cloth target. Furthermore, our results have indicated considerable potential for developing even more efficient devices based on a clear understanding of tsetse flight behaviour around artificial objects. Odour-baited blue and black objects of about 1 m in size are clearly attractive to *G. swynnertoni*, even when stationary. The main remaining deficiency in these artificial devices is that they fail to catch many flies that visit the vicinity of the trap, and most probably, also land on the outside surfaces.

Natural host odour cues are particularly critical in initiating investigation of artificial objects by tsetse (Hargrove, 1980a,b), and hence, facilitating capture in traps, or contact with insecticide-impregnated targets. For example, the presence of carbon dioxide increased the numbers of *G. m. morsitans* landing on black and blue targets by up to four times in Zimbabwe (Green, 1993). Many years ago, Hargrove (1980a) also demonstrated that the odour of a single ox could increase the absolute number of *G. m. morsitans* and *G. pallidipes* visiting a black cylindrical model by 4–7 times. Landing behaviour also differed with each manipulation of model size and the presence / absence of host odours.

After many years of similar work with *morsitans* tsetse, it seems unlikely that improvements in target / trap performance can be achieved by using conventional tsetse attractants, other than carbon dioxide (Green, 1993; Torr *et al*., 1995; Groenendijk & Takken, 1996). Similar results have been reported in the search for novel odour cues from a critical preferred host, the wart hog (Torr, 1994). While studying behaviour in the vicinity of live and stuffed wart hogs, Torr (1994) found that subtle features of the adult wart hog's head (dark glandular patches near the eyes) are critical for attractiveness. These sorts of visual cues based on natural behaviour should be taken into consideration in the design of artificial devices.

Altogether, visual cues seem to have considerable untapped potential for the development of more efficient attractive devices. This potential has been shown in many studies on the attraction of tsetse to simple objects of different colours, shapes and sizes (Green, 1986, 1988, 1994). Visual cues are critical in the design of traps, as traps obviously perform their function only if flies orient to entrances, and if they investigate features of the trap's non-return system. Hence, improved traps for savannah tsetse such as the M3 in Zimbabwe (Mhindurwa, 1994) and the S-traps reported here have incorporated multiple entrances in an attempt to catch more flies. If properly designed (each entrance can also be an exit), this approach to trap improvement can facilitate entry, and presumably improve efficiency, but only if the attractiveness of the object as a whole is not compromised.

Our experiments with sticky materials and radial electric nets suggest that the main problem with improving trap efficiencies for members of the *morsitans* group is finding a balance between enticing flies to investigate large, blue attractive objects, while simultaneously guiding them into a small, confined area with limited exit possibilities. Given the number of flies that clearly escape capture, it should be possible to produce a large increase in catch if flies can be discouraged from landing on outside trap surfaces. To facilitate trap investigation and enhance entry responses, more innovative trap formats should be tried, paying close attention to entrance design (especially shape, size, height and contrast features).

It should be possible to manipulate fly entry behaviour in traps through a creative combination of attractive and repellent stimuli. This approach may require the study of features not apparent to the human eye, but detected by tsetse (ultraviolet and polarized light, Green, 1994). For example, trap materials could be manipulated in terms of colour, shape, texture and shininess to provide a 'push–pull' stimulus, discouraging landing behaviour on an outside attractive surface, while simultaneously encouraging entry behaviour on an inner entrapping surface. This has already been the philosophy behind the use of blue (attraction) and black (landing) cloth in attractive devices, but it has not been pursued with much sophistication. If combined with further research on close-range attractants, traps could become much more than just monitoring tools and could potentially become practical alternatives for the large-scale control of many species of savannah tsetse.

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