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Tsetse and other biting fly responses to Nzi traps baited with octenol, phenols and acetone

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Abstract. Octenol (1-octen-3-ol), acetone, 4-methylphenol, 3-n-propylphenol, and other potential attractants (human urine, stable fly faeces), as well as guiacol, creosol (potential repellents), were tested as baits for biting flies in North America using standard phthalogen blue IF3GM cotton Nzi traps, or similar commercial polyester traps. Baits were tested during the summers of 2001–04 at a residence in Canada and during January–August 2001 at a dairy in the U.S.A. Behaviour in the presence of octenol was also studied by intercepting flies approaching a trap through the use of transparent adhesive film. Analogous bait and/or trap comparisons were conducted in natural settings in June 1996 in Kenya and in September–December 1997 in Ethiopia. In Canada, catches of five of six common tabanids (*Tabanus similis* Macquart, *Tabanus quinquevittatus* Wiedemann, *Hybomitra lasiophthalma* [Macquart], *Chrysops univittatus* Macquart, *Chrysops aberrans* Philip) and the stable fly *Stomoxys calcitrans* L. were increased significantly by 1.2–2.1 times with octenol (1.5 mg/h). Catches of *T. quinquevittatus* and *S. calcitrans* were 3.5–3.6 times higher on a sticky enclosure surrounding a trap baited with octenol. No other baits or bait combinations had an effect on trap catches in North America. In Ethiopia, standard Nzi traps baited with a combination of acetone, octenol and cattle urine caught 1.8–9.9 times as many *Stomoxys* as similarly baited epsilon, pyramidal, NG2G, S3, biconical and canopy traps, in order of decreasing catch. When baits were compared, catches in Nzi traps of six stable fly species, including *S. calcitrans*, were not affected by octenol (released at approximately 1 mg/h), or cattle urine (140 mg/h), used alone or in combination with acetone (890 mg/h). Acetone alone, however, significantly increased the catches of common *Stomoxys* such as *Stomoxys niger niger* Macquart, *Stomoxys taeniatus* Bigot, and *S. calcitrans* by 2.4, 1.6 and 1.9 times, respectively. Catches of *Glossina pallidipes* Austen were increased significantly in traps baited with acetone, urine or octenol, or any combination, relative to those in unbaited traps (1.4–3.6x). Catches of *Glossina morsitans submorsitans* Newstead were increased significantly by 1.5–1.7 times, but only when baits were used individually. Unlike other studies with East African tsetse, catches of both tsetse species with the complete bait combination (acetone, urine and octenol) did not differ from those in unbaited traps. Experiments with an incomplete ring of electric nets surrounding a Nzi trap, and a new approach using a sticky enclosure made from transparent adhesive film, revealed diverse responses to artificial objects and baits among biting flies. In Kenya, daily trap efficiency estimates for traps baited with either carbon dioxide (6 L/min) or a combination of acetone, cattle urine and octenol were 21–27% for *G. pallidipes*, 7–36% for *Glossina longipennis* Corti, 27–33% for *S. n. niger*, and 19–33% for *Stomoxys niger bilineatus* Grünberg, assuming 100% electrocution efficiency. Actual trap efficiencies

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may have been lower, given observed outside : inside electric net catch ratios of 0.6 : 1.6. Observed ratios averaged 54% of expected values, with 10 of 15 possible ratios less than the minimum possible value of 1.0.

Key words. *Glossina*, *Stomoxys*, Tabanidae, acetone, baits, Nzi trap, octenol, phenols.

Introduction

The discovery of potent attractants for tsetse in the 1980s, along with research on visual ecology (Gibson & Torr, 1999), set the stage for the development of cost-effective bait technologies for tsetse control (Vale & Torr, 2004). Similar practical systems for other biting flies have yet to emerge, despite the improved catches of tabanids and stable flies that can be achieved with the use of the novel baits derived from research on tsetse (French & Kline, 1989; Holloway & Phelps, 1991; Phelps & Holloway, 1992). Since Gibson & Torr (1999), researchers have continued to test novel attractants for their efficacy for biting flies (Hayes *et al.*, 1993; Djiteye *et al.*, 1998; Nilssen, 1998; Cilek, 1999; Mohamed-Ahmed & Mihok, 1999; Kristensen & Sommer, 2000; International Atomic Energy Agency [IAEA], 2003; Birkett *et al.*, 2004; Krčmar *et al.*, 2005, 2006). Baits such as 1-octen-3-ol (octenol), acetone, 4-methylphenol, 3-n-propylphenol and aged urine from bovines are just a few examples of materials that have potential for attracting biting flies (IAEA, 2003).

Based on similar blood-feeding and host-seeking behaviours, bait technologies should ultimately be applicable to the control of biting flies other than tsetse. However, this approach may be practical only if the visual cues that attract flies to traps or targets can be optimized (Green, 1994; Hall & Wall, 2004) and if economical baits can be developed to improve range and efficiency of attraction. For tsetse such as *Glossina pallidipes* Austen, the range of attraction to a natural point source odour such as that of an ox may be as high as 90 m, or in the order of 45 m for simple baits (Vale, 1980, 1984). Similarly, an efficient phthalogen blue and black cloth trap for this species, the NG2G, with baits such as acetone, aged cattle urine and octenol may catch as many as 47% of the flies approaching at close range (Dransfield & Brightwell, 2001). By contrast, similar general purpose cloth traps catch few biting flies without the use of impractical baits such as CO_2 (Mohamed-Ahmed & Mihok, 1999).

To follow up on the many insights gained into biting fly behaviour from research on tsetse, bait trials were initiated in North America using the Nzi trap, which has been found to give excellent catches of biting fly species (Mihok, 2002; Mihok *et al.*, 2006). Experiments with sticky enclosures and/or electric nets were also conducted in Africa and North America to investigate the visual and olfactory responses of biting flies. The overall objective of these studies was to explore the usefulness of attractive bait technologies refined in the tropics for temperate species and environments.

Materials and methods

New or nearly new Nzi traps made from phthalogen blue and black cotton and white polyester mosquito netting were used as standard traps (Mihok *et al.*, 2006), unless stated otherwise. During experiments, traps or baits were rotated every 24 h, typically on consecutive days, and catches were tallied on a daily basis. Trials in Africa were conducted at Chanka, Ethiopia (8°43′N, 35°8′E) in a grazed woodland with villagers and cattle present, and at Nguruman, Kenya (0°03′S, 36°10′E) in a natural woodland with minimal human activity. Trials in North America were conducted at a 50-cow dairy in Gainesville, Florida (29°41′N, 82°16′W), and at a residence next to farmland on the edge of the village of Russell, Ontario (45°15′N, 75°21′W).

Baits and release rates were selected to be representative of common practices for tsetse, tabanids and stable flies (reviewed by Gibson & Torr, 1999). Unless stated otherwise, chemicals were reagent-grade (98%) from Sigma-Aldrich (St. Louis, MO, U.S.A.). Release rates were adjusted by using polyethylene sachets with different surface areas (Torr *et al.*, 1997), or bottles with different apertures. The chemicals tested were acetone (A, commercial grade), 1-octen-3-ol (octenol or O), 4-methylphenol (4MP), 3-n-propylphenol (3PP, Ujváry *et al.*, 2002), 2-methoxyphenol (guiacol), and 2-methoxy-4-methylphenol (creosol). Release rates for phenols (multiple sachets) were measured in Florida in a laboratory fume hood over several weeks at room temperature; other values were obtained in the field. In Africa, 86% octenol was used (International Flavours & Fragrances, London, U.K.). In North America, a consumer formulation in a wax base was used (Dragonfly® lure; Biosensory, Willimantic, CT, U.S.A.) with a release rate of 1.5 mg/h at 27 °C (manufacturer). The Mosquito Magnet® octenol cartridge (American Biophysics, East Greenwich, RI, U.S.A.) was also tested. From its octenol content and recommendations for replacement at 21 days, the release rate should have been 5.4 mg/h.

In Africa, acetone, urine and octenol were dispensed as for sampling savannah tsetse (Kyorku *et al.*, 1990; Baylis & Nambiro, 1993; Mihok *et al.*, 1996a; Brightwell & Dransfield, 1997). At Nguruman, acetone was released at 2500 mg/h (500 mL bottle, 7 cm aperture), urine at 200 mg/h (2 cm aperture), and octenol at 1 mg/h (20 mL vial, 3 mm aperture). Urine was aged for 2 weeks to develop phenolic components (Okech & Hassanali, 1990). At Chanka, release rates were 890 mg/h for acetone and 140 mg/h for urine. Due to the lack of electricity at this remote site, we were unable to obtain onsite measurements for octenol. In different seasons in similar habitat in Kenya,

octenol release rates with this dispenser are 1.0 mg/h ± 0.2 (standard error [SE], $n = 20$).

In Florida, sponges impregnated with stable fly faeces were tested based on laboratory observations of attraction to faeces (Carlson *et al.*, 2000). Baits were prepared by suspending moistened sponges in a stable fly colony for 3 days until they were black. A single bait consisted of four moistened sponges (each 11 × 4 × 0.5 cm) replaced every second day.

An outline of experiments is presented in Table 1, with further details provided below.

Africa

Experiment 1. This experiment was designed to investigate the performance of similarly baited traps relative to a standard Nzi trap in an area with many *Stomoxys*, an objective not fully achieved during development of the Nzi trap (Mihok, 2002). In September 1997, 21 traps, each baited with a combination of acetone (A), cattle urine (U) and octenol (O), were set 50–100 m apart at Village 12 near Chanka, West Wollega, Oromia, Ethiopia in three 7 × 7 Latin squares, with a baited Nzi trap as the control. The other traps were the biconical (Challier *et al.*, 1977), pyramidal (Gouteux & Lancien, 1986), NG2G (Brightwell *et al.*, 1991), canopy (Hribar *et al.*, 1991), S3 (Ndegwa & Mihok, 1999), and epsilon (Hargrove & Langley, 1990) traps. All traps were made from phthalogen blue and black cotton, with white polyester mosquito netting.

Experiment 2. After confirming excellent performance for several *Stomoxys* spp. in experiment 1, 24 standard Nzi traps were set in three 8 × 8 Latin squares at the same location to test single baits and combinations of octenol, cattle urine and acetone relative to an unbaited trap: O, U, A, OU, OA, AU, AUO. The objective was to investigate how Ethiopian species at high altitude (1290 m a.s.l) react to AUO (Slingenbergh, 1992; Belete *et al.*, 2004).

Experiment 3. This qualitative experiment was conducted in the vicinity of Nguruman, Kenya, a site with a history of community-based tsetse control (Dransfield & Brightwell, 2004). A polyester Nzi trap ('pure blue' fabric 24, Mihok, 2002) from the Vestergaard Frandsen Group (Kolding, Denmark) was used. Nzi traps made from this material caught as many biting flies as a standard trap at Nguruman (experiment 23, Mihok, 2002).

In June 1996, four woodland sites were selected to investigate responses to baited Nzi traps in terms of attraction vs. efficiency. The four sites were chosen based on daily catches over 5 days in AUO-baited Nzi traps set at 10 sites. The best sites were set with contrasting baits or catching devices for 3 days during fair weather (Table 2 shows site/day contrasts). One objective was to document fly behaviour in the presence of attractants, but in the absence of a trap. This was done by erecting nominally 'invisible' sticky enclosures about the same size as a trap to intercept flies investigating a point odour source (site 1 on all 3 days with different baits each day, and sites 2–3 on day 3 only for a simultaneous comparison of several baits). A second objective was to obtain coincident estimates of conventional trap efficiency using an incomplete ring of electric nets surrounding a baited Nzi trap (site 4 on all 3 days).

At site 1, a 1-m high, triangular sticky enclosure, 1-m in length on each side, was constructed by stacking three pieces of transparent fly control adhesive film (Rentokil FE 22/G; Agrisense, Pontyprid, U.K.), 37 cm wide with a 30-cm strip of adhesive) around three grey poles, leaving only a small gap between the pieces (Fig. 1). The enclosure was baited with AUO on day 1, left unbaited on day 2, and baited with O on day 3. On day 3, identical enclosures were erected at sites 2 and 3, separated by 500 m, for a complimentary comparison of catches with CO_2 or CO_2 + O. Carbon dioxide was released from hidden gas cylinders at 6 L/min from 05.30 hours to 19.15 hours. This ensured that early morning activity of *Glossina longipennis* Corti was monitored (sunrise at 06.33 hours). Other baits were in place for 24 h.

At site 4, 100-m away from site 1, over the 3 days during which the sticky enclosure(s) were operated, a Nzi trap was surrounded by an incomplete ring of six 1 × 1-m electric nets at a 6-m radius (Bonar Industries, Harare, Zimbabwe) (Dransfield & Brightwell, 2001). Flies in the trap and those electrocuted on the inside and outside net faces were tallied every 3 h, starting shortly after sunrise and ending in darkness. The trap was baited with AUO on days 1 and 3. On day 2, CO_2 only was released for a simultaneous comparison with the sticky enclosures variously baited with CO_2 and/or octenol at other sites. Trap efficiency was calculated using formula 1 of Dransfield & Brightwell (2001), given an interception fraction of 0.148 (fixed value from the geometry), and assuming 100% electrocution of flies hitting the nets. This calculation provides a relative index for comparison among studies with similar spatial configurations of electric nets and should not be interpreted as an absolute value. As large flies such as tsetse may not all be killed and retained on contact with electric nets (Dransfield & Brightwell, 2001), raw electric net catches are provided for other trap efficiency calculations based on alternative assumptions or methods.

Ontario

Experiments in Ontario focused on readily available retail products and several phenols that might provide practical baits in a residential setting. Data were collected for *Stomoxys calcitrans* and many tabanid species. Nzi traps were set 7–25 m apart in the centre of a 0.5-ha turfgrass area. Traps were set facing west, unless stated otherwise. Standard phthalogen blue cotton Nzi traps were used, except for experiment 6 when traps in similar blue fabrics were also tested (Mihok *et al.*, 2006). The nearest farm animals were a few dairy cattle and horses 1 km away. Hourly weather data were obtained from Environment Canada for Ottawa airport (22 km WNW) for interpretation of results.

Experiment 4. Two Nzi traps, both facing east, were set in 2002 with a Dragonfly® octenol lure rotated among sites in 2 × 2 Latin squares during mid-summer (average daily maximum temperature 28°C). The control was an unbaited trap. This retail octenol lure was, and continues to be, widely available for use with propane-powered mosquito traps (Kline, 2002).

Experiment 5. Four Nzi traps, two facing east and two facing west, were set in 4 × 4 Graeco-Latin squares with an unbaited trap as the control. The treatments were a Dragonfly® octenol

Table 1. Outline of experiments testing baits and/or traps conducted at Chanka, Ethiopia; Nguruman, Kenya; Russell, Canada, and Gainesville, U.S.A.

Experiment details						Experiment design				Contrasts	
Exp	Location	Month	Objective	Target	Format	Sites	Reps	N	Control	Baits	Traps
1	Ethiopia	Sept 1997	Compare Nzi to conventional tsetse and biting fly traps using typical tsetse bait combination	*Stomoxys*	Latin squares	21	3	21	AUO-baited Nzi trap	AUO (acetone, cattle urine and octenol)	Nzi Biconical Pyramidal NG2G Canopy, S3 Epsilon
2	Ethiopia	Dec 1997	Compare typical bait formulations for tsetse using Nzi traps	*Stomoxys* *Glossina*	Latin squares	24	3	24	Unbaited trap	Single baits and combinations of acetone, cattle urine and octenol	Nzi
3	Kenya	June 1996	Compare Nzi traps, sticky enclosures and incomplete ring of electric nets	*Stomoxys* *Glossina* Non-biting muscids	Sequential contrasts over 3 days	4	N/A	N/A	AUO -baited Nzi traps set for 5 days at 10 sites before experiment	AUO Octenol CO_2 Octenol + CO_2	Nzi and other devices
4	Canada	July–Aug 2002	Test retail octenol formulation	Tabanidae *Stomoxys*	Latin squares	2	14	28	Unbaited trap	Dragonfly® octenol lure	Nzi
5	Canada	June 2003	Compare baits and east/west trap orientation	Tabanidae *Stomoxys*	Graeco- Latin squares	4	4	16	Unbaited trap facing east	Dragonfly® octenol lure Acetone Human urine	Nzi
6	Canada	Aug 2003	Compare retail octenol lures	Tabanidae *Stomoxys*	Latin squares	6	4	24	Dragonfly® octenol lure	Dragonfly® Mosquito Magnet®	Nzi
7	Canada	July 2004	Compare various phenols (with octenol) to octenol alone	Tabanidae *Stomoxys*	Latin squares	6	1	6	Dragonfly® octenol lure	Dragonfly® octenol lure 4MP + 3PP Guiacol, Creosol	Nzi
8	Canada	July–Aug 2004	Compare phenols ± acetone (with octenol) to octenol alone	Tabanidae *Stomoxys*	Sequential randomized blocks	1	12	12	Dragonfly® octenol lure	Dragonfly® octenol lure 4MP + 3PP 4MP + 3PP + acetone	Nzi
9	Canada	Sept 2004	As in Exp 7 but with a phenol treatment with acetone added	*Stomoxys*	Latin squares	6	1	6	Dragonfly® octenol lure	Dragonfly® octenol lure 4MP + 3PP 4MP + 3PP + acetone Guiacol, Creosol	Nzi
10	Canada	Aug 2002	Document fly behaviour at a baited or unbaited sticky enclosure with or without a Nzi trap present	Tabanidae *Stomoxys*	Sequential contrasts over 6 days	2	N/A	N/A	Matching catches in a baited or unbaited trap, catches before and after	Dragonfly® octenol lure	Nzi Sticky enclosure Nzi + sticky enclosure
11	U.S.A.	Feb–March 2001	Test SF faeces as a combination bait	*Stomoxys*	Latin squares	4	2 × 9	36	Low acetone	Low acetone + SF faeces Low acetone	Nzi
12	U.S.A.	Feb–March 2001	Test SF faeces as a combination bait	*Stomoxys*	Paired comparisons	4	37	37	Unbaited trap	Low acetone + SF faeces	Nzi
13	U.S.A.	Jan–Feb 2001	Test low acetone + octenol with two kinds of trap	*Stomoxys*	Paired comparisons	4	2 × 9	18	Unbaited trap	Dragonfly® octenol lure + low acetone	Nzi Vavoua
14	U.S.A.	April–May 2001	Test SF faeces as a combination bait at higher acetone release rate, test heartbeat sound	*Stomoxys*	Latin squares	4	4	16	Unbaited trap	High acetone+ SF faeces High acetone Bugjammer sound	Nzi
15	U.S.A.	July–Aug 2001	Test high acetone, best phenol and combined bait	*Stomoxys*	Latin squares	4	9	36	Unbaited trap	High acetone 4MP 4MP + high acetone	Nzi

Exp, experiment; Reps, replicates; *n,* sample size per treatment; N/A, not applicable (qualitative experiment); AUO, acetone, urine and octenol; 4MP, 4-methylphenol; 3PP, 3-n-propylphenol; SF faeces, stable fly faeces impregnated sponges.

Table 2. Catches of tsetse and other flies in Nzi traps at Nguruman, Kenya in experiment 3 compared with those on transparent triangular sticky enclosures, and trap efficiency estimates for a Nzi trap enclosed in an incomplete ring of electric nets. Catches of *Stomoxys* at sites 2 and 3 are in parentheses; these numbers should be interpreted in terms of site differences found during the initial site survey with traps.

Device	Bait	Site	Day	*Glossina pallidipes*	*Glossina longipennis*	*Stomoxys niger niger*	*Stomoxys bilineatus niger*	Non-biting muscids
Initial site survey, catches in similarly baited Nzi traps								
Catches*	AUO	All		230 ± 306	24 ± 37	67 ± 238	18 ± 58	16 ± 32
Maximum				757	78	597	153	105
Ratio of site catch to catch at site 1								
	2			0.73	1.22	0.04	0.08	0.80
	3			0.66	1.41	0.09	0.23	0.84
	4			1.21	0.60	1.04	0.79	0.51
Transparent triangular sticky enclosures with no trap inside								
Enclosure	AUO	1	1	489	34	599	137	70
Enclosure	Unbaited	1	2	23	1	623	39	24
Enclosure	O	1	3	34	1	1133	251	47
Enclosure	CO_2	2	3	123	38	(1020)	(124)	980
Enclosure	CO_2 + O	3	3	315	265	(473)	(138)	538
Nzi trap enclosed in an incomplete ring of electric nets								
Nzi trap	AUO	4	1	536	27	336	36	25
Net, In				302	7	99	11	301
Net, Out				156	9	81	15	270
Efficiency				21%	36%	33%	33%	1%
Nzi trap	CO_2	4	2	368	14	768	185	87
Net, In				151	28	304	66	215
Net, Out				127	21	395	76	202
Efficiency				27%	7%	27%	29%	6%
Nzi trap	AUO	4	3	878	43	483	28	24
Net, In				345	31	169	18	332
Net, Out				164	10	137	43	226
Efficiency				27%	17%	30%	19%	1%

*Mean ± 2 standard deviations ($n = 50$).
In, inside net face; Out, outside net face.

lure, very high acetone (2700 mg/h) and aged human urine (50 mg/h).

Experiment 6. Six minor blue cloth variations on Nzi traps were rotated among sites in 6 × 6 Latin squares with two controlled-release retail formulations of octenol (Dragonfly® and Mosquito Magnet®) rotated among sites as a second experimental factor.

Experiment 7. Six Nzi traps were set in a single 6 × 6 Latin square at peak tabanid numbers. All traps were baited with a Dragonfly® octenol lure; hence the control was an octenol-baited trap. The treatments were: O + low phenols (4MP 9.9 mg/day + 3PP 6.6 mg/day), O + medium phenols (4MP 19.8 mg/day + 3PP 2 mg/day), O + high phenols (4MP 19.8 mg/day + 3PP 6.6 mg/day), O + creosol (26 mg/day), O + guiacol (28 mg/day). The phenols and their release rates were chosen according to studies of the roles played by 4MP and 3PP in attracting tsetse to cattle urine (Hassanali *et al.*, 1986; Bursell *et al.*, 1988); two potential repellents (guiacol, creosol) were also included for contrast (Torr *et al.*, 1996; Ujváry *et al.*, 2002).

Experiment 8. Three bait treatments were rotated at a single Nzi trap in sequential randomized blocks to eliminate confounding effects from the simultaneous presence of multiple baits, as in experiment 7. The control was an octenol-baited trap; the two treatments were: O + high phenols (4MP 19.8 mg/day + 3PP 6.6 mg/day), and the same combination with a high (H) release rate of acetone (560 mg/h), abbreviated as HA + O + high phenols.

Experiment 9. Experiment 9 was a repetition of experiment 7 during the peak stable fly season, with one change: the O + medium phenols treatment was dropped. It was replaced with a low release rate of acetone (60 mg/h) plus octenol plus phenols (LA + O + high phenols).

Experiment 10. This experiment was set at the two sites in experiment 4 by pausing the experiment for 6 days. The objective was to investigate orientation to trap components in the presence and absence of octenol by intercepting flies approaching a trap at very close range. A complete sticky enclosure was used based on comparisons of complete and incomplete configurations of electric nets in Dransfield & Brightwell (2001). At one site (experimental treatment), we completely surrounded a standard Nzi trap (Fig. 2) with an overlapping triangular wall of adhesive film. At the other site 25 m away (control), film without adhesive was pinned to the front of a standard Nzi trap; the film covered everything except the entrance.

The sticky enclosure was constructed to intercept all flies approaching from ground level to the bottom edge of the cone (1 m high). The sticky wall was 1.5 m wide on each side, with a 10-cm gap between the sticky wall and the bottom edge of the cone. Only flies approaching from above 1 m could potentially

Fig. 1. Sticky enclosure made from transparent Rentokil fly control adhesive film in Kenya. Baits under a small metal cover are visible in the bottom right corner.

gain access to the trap through this small gap. Each site was baited with octenol on alternate days for 6 days. Traps were set facing east so that flies flying upwind into the expected odour plume would encounter the front of the trap first. On days 5–6, the trap was lifted out of the enclosure to document behaviour in the absence of a visual target, replicating the configuration in experiment 3 in Kenya. Catches were tallied to coincide with the shifting pattern of sunlight on the three sides of the trap: late morning (east, 09.00–12.00 hours), early afternoon (SW, 12.00–15.00 hours), late afternoon (SW−NW, 15.00–18.00 hours), evening (NW, 18.00–21.00 hours), and night/early morning (east, 21.00–09.00 hours).

Fig. 2. Side view of the Nzi trap enclosed in a continuous wall of transparent Rentokil fly control adhesive film in Ontario. A Dragonfly® octenol lure hangs at the back corner.

Florida

Experiments in Florida focused on several baits (stable fly faeces, acetone, octenol, phenols) that might be considered by farmers looking for pest control solutions in an applied setting, as well as a single test of an alternative trap (the Vavoua). Experiments targeted wild *S. calcitrans* only. A retail version of the Nzi trap in royal blue and black polyester sold in 2001–02 by Vestergaard Frandsen was used (Mihok *et al.*, 2006). Sites were 25–50 m apart. A stable fly research colony was used to prepare faeces baits (Carlson *et al.*, 2000).

Experiment 11. Four Nzi traps were set for 18 days during February–March 2001. They were baited with a low release rate of acetone (80 mg/h) based on Cilek (1999), or acetone plus stable fly faeces-impregnated sponges in 2 × 2 Latin squares.

Experiment 12. Four Nzi traps were set in paired comparisons of traps baited with acetone plus stable fly faeces-impregnated sponges vs. unbaited traps.

Experiment 13. Two Nzi and two Vavoua traps (Laveissière & Grébaut, 1990), of the same polyester fabrics, were set in paired comparisons of traps baited with acetone plus an octenol lure vs. unbaited traps. Vavoua traps were tested based on previously demonstrated good performance for several *Stomoxys* in Kenya (Mihok *et al.*, 1995, 1996b) and for *S. calcitrans* in Canada (Mihok *et al.*, 2006).

Experiment 14. Four Nzi traps were set in 4 × 4 Latin squares, with an unbaited trap as the control. Two of the treatments were as in experiment 11, but with a higher release rate of acetone (250 mg/h). The third treatment was a Nzi trap baited with a device (Tam, 2003) that produces a simulated heartbeat (US patent #6 568 123, Bugjammer Pro; Bugjammer Inc., Pennington, NJ, U.S.A.).

Experiment 15. Four Nzi traps were set in 4 × 4 Latin squares, with an unbaited trap as the control. The treatments were acetone (A, 250 mg/h), 4-methylphenol (4MP, 9.9 mg/day), and a combination of both (A + 4MP). 4MP is the key attractive phenol in cattle urine (Gibson & Torr, 1999).

Statistical analyses

Daily tallies of catches x were transformed as $y = log(x + 1)$ for ANOVA of experiments with baits and/or traps. The outcome of interest was an a priori significant change in catch relative to the control, e.g. an unbaited or a baited Nzi trap as specified in each experiment. Proportionate changes in catch were summarized as the response ratio (R) of each treatment relative to the control (Hedges *et al.*, 1999), i.e. the ratio of the detransformed

mean catch in the test trap to that in the standard. This measure of effect size in meta-analysis is the equivalent of the 'catch index' or 'index of increase' in entomological publications (Dransfield & Brightwell, 1992). Treatment results are presented in terms of *R* (lower 95% confidence interval [CI]–upper 95% CI), with geometric mean catches for the control ($GM_T = R \cdot GM_C$) also provided for interpretation. For the sticky enclosure in experiment 10, chi-square analyses were used to test for non-random landing on corresponding sides or surfaces of the trap. This calculation was made from observed tallies on the adjacent adhesive film relative to expected tallies based on a random distribution, as set by the physical areas being considered.

Results

Africa

Trap comparisons in experiment 1. High numbers of several *Stomoxys* spp. were captured at Chanka in the rainy season (total $n = 13\ 440$); these included 59% *Stomoxys niger niger* Macquart (44% male), 21% *Stomoxys taeniatus* Bigot (37% male), 17% *S. calcitrans L.* (25% male), 2% *Stomoxys niger bilineatus* Grünberg (36% male), 1% *Stomoxys boueti* Roubaud (33% male), and 0.2% *Stomoxys inornatus* Grünberg. The Nzi trap caught significantly more *Stomoxys* of all kinds than all other traps in nearly every comparison, with 1.8–1.9 times as many *Stomoxys* captured in the Nzi trap relative to the next best alternative, the epsilon ($GM_{Nzi} = 176$ vs. $GM_{epsilon} = 96$, arithmetic means of 213 vs. 112). The epsilon trap was the only trap that caught statistically equivalent numbers of some species of *Stomoxys* (common species shown in Fig. 3). For example, the 95% CI for *Stomoxys* in the epsilon trap just overlapped with the catch in the Nzi trap ($R = 0.55$, 0.30–1.01). Trends were similar among species and also by sex.

Baits in experiment 2. Stomoxys were still present during the dry season in high numbers ($n = 7\ 093$) with a similar species and sex composition: 60% *S. n. niger* (45% male), 20% *S. calcitrans* (31% male), 10% *S. taeniatus* (51% male), 8% *S. niger bilineatus* (30% male), 1% *S. inornatus* (41% male), and 0.4% *S. boueti*. Only traps baited with acetone alone caught significantly more *Stomoxys (*2.3-fold) than unbaited traps (Fig. 4, $GM_{acetone} = 29.8$ vs. $GM_C = 12.6$). Trends were similar by species and by sex, with response ratios for common *Stomoxys* for the acetone treatment of 2.4 (*S. n. niger*), 1.6 (*S. taeniatus*) and 1.9 (*S. calcitrans*). Data on the responses of two tsetse at low numbers were also obtained (*G. pallidipes*, $n = 857$, *Glossina morsitans submorsitans* Newstead, $n = 536$; both with $GM_C = 2.1$). Catches were increased significantly with each bait on its own in both tsetse, with the largest increase for *G. pallidipes* and cattle urine alone (3.6-fold). Catches were increased significantly for *G. pallidipes* in dual bait combinations containing any two of the three baits, but not for *G. m. submorsitans* (Fig. 4). Catches of both tsetse species with the complete bait combination (AUO) were not significantly different from those in unbaited traps.

Sticky enclosures in experiment 3. With the exception of low numbers of *Stomoxys* at sites 2 and 3 (4–23% of those at site 1 for two *S. niger* subspecies), baseline trap catches of all other flies at the four sites prior to the experiment differed on average by only ± 27% relative to site 1 (Table 2). At site 1 on days 1 and 2 of the 3-day experiment, catches of *Stomoxys* on an unbaited or an AUO-baited enclosure were similar to the maximum catch in AUO-baited traps. At sites 1–3 on day 3, catches of *Stomoxys* on baited enclosures were 2.1-fold (O), 1.7-fold (CO_2) and 0.9-fold (CO_2 + O) those of the unbaited enclosure. Given the large site differences in baseline catches of *Stomoxys*, the relative catch ratios at sites 2 and 3 with CO_2 or CO_2 + O vs. site 1 with octenol may have been much higher than indicated by raw catch ratios. Catches of non-biting muscids in unbaited

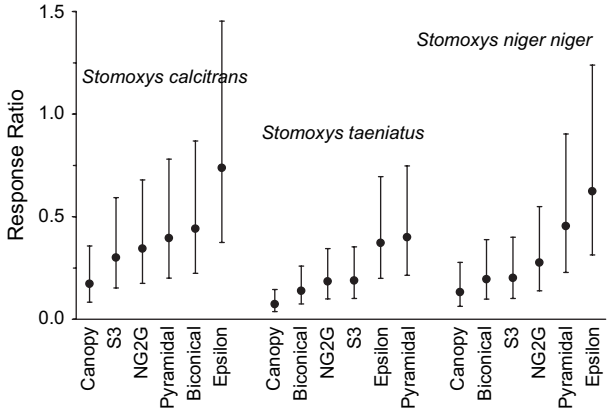

Fig. 3. Response ratios ($R \pm 95\%$ confidence interval [CI] in experiment 1 in Ethiopia for common *Stomoxys* spp. for various traps relative to the Nzi trap ($n = 21$ per trap except for the Canopy, $n = 16$, and Biconical, $n = 20$). Geometric mean catches (GM, flies/trap/day) in Nzi traps were 91.3 (*Stomoxys niger niger*), 34.4 (*Stomoxys taeniatus*) and 20.7 (*Stomoxys calcitrans*). Differences relative to a Nzi trap are significant when the CI does not overlap with 1.

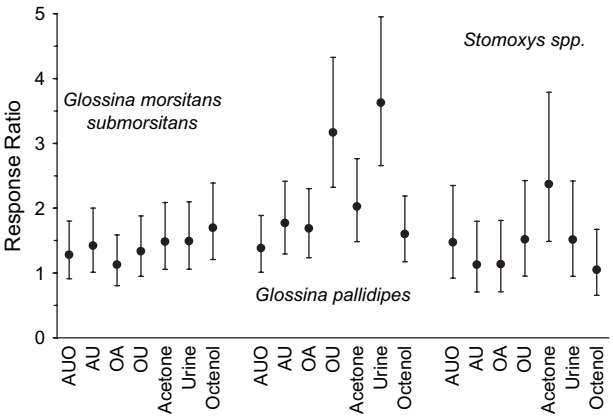

Fig. 4. Response ratios ($R \pm 95\%$ confidence interval [CI]) in experiment 2 in Ethiopia for stable flies (*Stomoxys* spp.) and tsetse (*Glossina pallidipes, Glossina morsitans submorsitans*) in Nzi traps baited with combinations of octenol (O), cattle urine (U) and acetone (A) relative to an unbaited Nzi trap ($n = 24$ per trap). Differences relative to an unbaited trap are significant when the CI does not overlap with 1.

(24), O-baited (47) and AUO-baited (70) enclosures were similar to those in AUO-baited traps (mean 16, maximum 105). The effect of CO_2 on non-biting muscids was unambiguous, with large increases in catch relative to an unbaited enclosure (CO_2: 40.8-fold; CO_2 + O: 22.4-fold).

Few *G. pallidipes* (23–34) were caught on an unbaited or an O-baited sticky enclosure; enclosures baited with CO_2, CO_2 + O or AUO caught about as many *G. pallidipes* (123–489) as baited traps (mean 230, maximum 757). Similarly, very few *G. longipennis* (one) were caught on an unbaited or an O-baited sticky enclosure; enclosures baited with CO_2 or AUO caught about as many G. longipennis (34–38) as baited traps (mean 24, maximum 78). Unprecedented numbers of *G. longipennis* (265) were captured with CO_2 + O, with 97% of the catch obtained during the sunrise peak in activity (05.50–07.00 hours). Tens of thousands of small Diptera were also captured with CO_2 + O but were not identified.

Tabanids were rare when this experiment was conducted (mean of 1.8/trap/day). Only one tabanid was caught on an unbaited enclosure; 9–26 were caught on baited enclosures (mostly *Haematopota* Meigen). *Stomoxys* were typically caught feet-first on the adhesive film; tsetse and tabanids were found in various positions. Flies of all kinds were caught in the greatest numbers (75–87%) on the lowest of the three tiers of adhesive film.

Electric nets in experiment 3. Catches over 3 days in the Nzi trap surrounded by electric nets at site 4, baited with AUO or CO_2, were similar to the AUO-baited sticky enclosure, and were within the range of catches with AUO-baited traps during baseline trapping, with two exceptions (Table 2). On day 2, catches of *S. niger* subspecies were higher than the maximum previous trap catch (768 + 185 vs. 597 + 153); this was also the case on day 3 for *G. pallidipes* (878 vs. 757). Very low trap efficiency was found for non-biting muscids with AUO *(*1%); efficiency was 6% with CO_2. Pooled daily estimates of efficiency for other species were 21–27% for *G. pallidipes*, 7–36% for *G. longipennis*, 27–33% for *S. n. niger*, and 19–33% for *S. n. bilineatus*, with no obvious pattern. For the two large samples, efficiency estimates pooled over all 3 days were higher for males than for females (*G. pallidipes*, 31% vs. 21% efficiency, $n = 1782$ in traps, 44% males; *S. n. niger*, 34% vs. 25% efficiency, $n = 1587$ in traps, 54% male). Mean outside net to inside net catch ratios varied from 0.6 to 1.6, relative to expected ratios of 1.2 to 7.1. On average, observed outside : inside net ratios were 54% of expected values; a less than 100% electrocution efficiency may have contributed to this result (Griffiths & Brady, 1994). However, with 10 of 15 observed ratios lower than the minimum possible value of 1.0 (more flies cannot leave than arrive), it is likely that several other factors related to this experimental protocol contributed to these results (Dransfield & Brightwell, 2001).

Ontario

The total catch over 360 trap-days of effort was 2433 tabanids (53% *Tabanus* L., four spp.; 42% *Chrysops* (Meigen), 11 spp.; 5% *Hybomitra* Enderlein, four spp.), and 985 *S. calcitrans* (77% male). The catch of tabanids consisted almost entirely of females.

Octenol in experiments 4–6. Catches of stable flies and five of six tabanid species were significantly higher in traps baited with octenol (Fig. 5). Catches were significantly higher when traps faced east (experiment 4; tabanids: $R = 1.9$ [1.6–2.2], $GM_C = 11.4$; stable flies: $R = 1.8$ [1.5–2.2], $GM_C = 2.6$) or both east and west (experiment 5; tabanids: $R = 1.9$ [1.4–2.4], $GM_C = 5.5$). For tabanids, the best configuration was for an octenol-baited trap facing west ($R = 2.7$ [1.7–4.0]) relative to an unbaited trap facing in the same direction. Catches of tabanids with aged human urine (R 1.0−1.1), or acetone (R 0.8−1.2) were not significantly different from those in an unbaited trap. In experiment 6, catches were not significantly different with the two octenol lures for both tabanids and stable flies, pooled for minor trap variations (R 0.9−1.1).

Phenols in experiments 7–9. Catches of tabanids with octenol plus phenols in experiment 7 ($GM_C = 11.1$) and stable flies in experiment 9 ($GM_C = 5.7$) were not significantly different from those with octenol alone (Fig. 6). The addition of acetone at high (tested for tabanids only) or low (tested for stable flies only) release rates to the octenol plus high phenol combination did not significantly affect the catch. Catches of tabanids with O + 4MP + 3PP, with or without acetone in experiment 8 ($GM_C = 4.9$), were also not significantly different from those with octenol alone. Data not shown in Fig. 6 for stable flies at low numbers in experiment 7 ($GM_C = 1.3$) also indicated no significant differences in catch among baits ($F = 2.4$, d.f. = 5, 20; $P = 0.07$).

Sticky enclosure in experiment 10. In total, 549 tabanids (two males) and 791 stable flies (55% males) were captured. Tabanids were mostly *Tabanus quinquevittatus* Wiedemann (70%) and *Chrysops aberrans* Philip (20%). The sticky enclosure blocked capture, with the exception of *Chrysops*. Over 4 days, 13

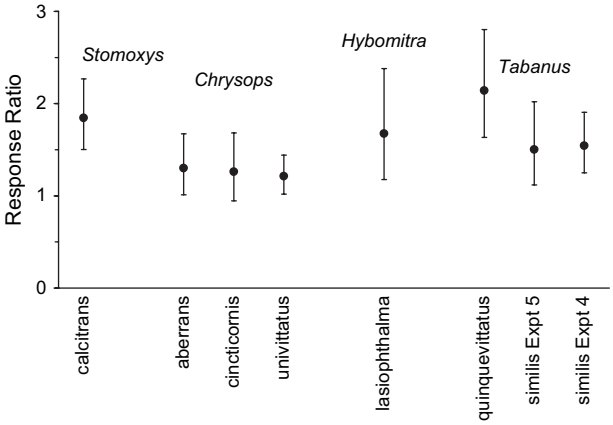

Fig. 5. Response ratios ($R \pm 95\%$ confidence interval [CI]) in Ontario in experiments 4 ($n = 28$) and/or 5 ($n = 16$) for stable flies (*Stomoxys calcitrans,* experiment 4 only), and tabanid species in Nzi traps baited with a Dragonfly® octenol lure relative to unbaited traps. Tabanids were *Tabanus similis* (both experiments), *Tabanus quinquevittatus*, *Chrysops aberrans*, *Chrysops univittatus* Macquart (experiment 4), and *Hybomitra lasiophthalma*, *Chrysops cincticornis* Walker (experiment 5).

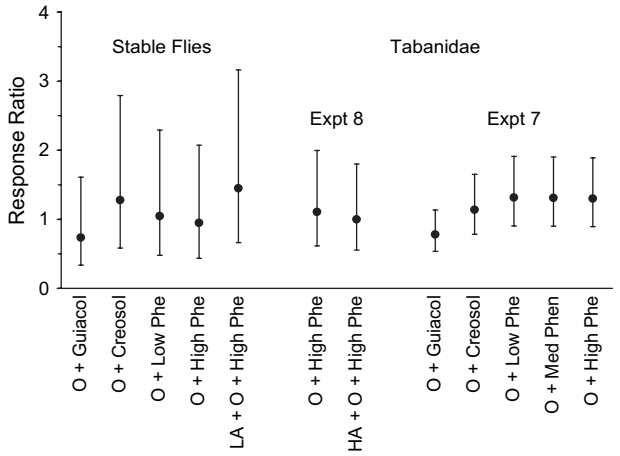

Fig. 6. Response ratios ($R \pm 95\%$ confidence interval [CI]) in Ontario in experiment 7 ($n = 6$) and experiment 8 ($n = 12$) for tabanids, and in experiment 9 ($n = 6$) for stable flies with various combinations and release rates of phenols and acetone in octenol-baited Nzi traps relative to traps baited with octenol alone. O, octenol; HA, high acetone; LA, low acetone; Phe, phenols (4-methylphenol + 3-n-propylphenol).

Chrysops entered through the small gap at the top. Simultaneously, 50 *Chrysops* were captured on the sticky enclosure, vs. 51 in the control trap. When a trap was not present inside the enclosure on days 5–6, only one *Chrysops* was captured on the adhesive film, compared with 26 in the control trap nearby. Mean trap catches of *Chrysops* for 6 days immediately before and after in the absence/presence of octenol were 10–26 flies/trap/day (Table 3).

During hot weather on days 1–3, catches of *T. quinquevittatus* were 3.6-fold higher (258 : 36) on the enclosure surrounding a trap with octenol than without octenol (Table 3). Only three *T. quinquevittatus* were caught on an unbaited enclosure at cooler temperatures on day 4. Between 48 and 257 stable flies were caught in the enclosure during these 4 days, with 3.5 times as many (508 : 145) caught in the enclosure with octenol than without octenol. On days 5 and 6 with no trap inside, 48 *T. quinquevittatus* and 118 stable flies were caught in the enclosure, relative to 0 and 49 in the control trap. Given the magnitude of sticky catches without a trap present relative to trap catches (Table 3), the adhesive film was clearly not invisible to biting flies.

The temporal and spatial pattern of catches was analysed in detail to investigate the effects of wind, sun and shade on fly behaviour towards trap surfaces. Winds were from the W/WNW/NNW in the afternoon when 74% of the flies were caught (Table 3). Hence, any flies orienting upwind to the octenol plume would have encountered the front of the trap first. For *T. quinquevittatus*, catches with octenol with a trap present inside the enclosure were non-random, with the highest proportional catch at the front of the trap (+ + east, $P << 0.001$; Table 4). For other configurations, the pattern was random. An octenol-related bias for the east, downwind side in the presence of a trap was significant for the period between 15.00 hours and 18.00 hours when the sun was falling on the back of the trap (Table 4). Catches with octenol and a trap present were also non-random for stable flies (+ + east, $P << 0.001$; Table 4), with significant deviations from a random pattern all afternoon (15.00 hours and 18.00 hours tallies). For the small sample sizes obtained for *Chrysops*, captures were random in all comparisons.

Sticky catches on the SW and NW sides were tallied for the three equal backgrounds (blue or black fabric, white netting). The catch distribution differed between *T. quinquevittatus* and stable flies ($\chi^2 = 20.9$, d.f. $= 2$; $P < 0.001$). Relative to an even distribution (33%), stable flies ($\chi^2 = 21.7$, d.f. $= 2$; $P < 0.001$, $n = 383$) were caught in proportionately greater numbers on blue (44%) vs. black (25%) or netting (31%). *T. quinquevittatus* ($\chi^2 = 9.6$, d.f. $= 2$; $P < 0.01$, $n = 175$) was caught in proportionately greater numbers on black (44%) vs. blue (31%) or netting (25%). At the front of the trap, catches were tallied on the three blue panels and by the entrance. Relative to an even distribution (25%), *T. quinquevittatus* ($\chi^2 = 43.2$, d.f. $= 3$; $P << 0.001$, $n = 122$) was caught in proportionately greater numbers at the entrance (44%) vs. the shelf (2%) and the two wings (22%, 31%, respectively). Stable flies ($\chi^2 = 79.0$, d.f. $= 3$; $P << 0.001$, $n = 270$) were caught in proportionately greater numbers on the wings (41%, 34%) vs. the shelf (21%), or the entrance (5%).

From the total sticky catches associated with vertical panels of fabric or netting (three equal 0.3-m wide sticky sectors, 1 m high), stable flies were caught in proportionately greater numbers in the middle and high sectors (20% low, 41% middle, 40% high; $\chi^2 = 49.5$, d.f. $= 2$; $P << 0.001$, $n = 584$). *T. quinquevittatus* was caught in proportionately greater numbers in the low and middle sectors (48% low, 38% middle, 14% high; $\chi^2 = 41.6$, d.f. $= 2$; $P << 0.001$, $n = 240$). *Chrysops* was caught in proportionately greater numbers in the higher sectors (12% low, 28% medium, 60% high; $\chi^2 = 16.7$, d.f. $= 2$; $P << 0.001$, $n = 50$). *Chrysops* was also seen landing on the cone of the trap. Stable flies, as well as *Chrysops*, were mostly caught feet-first on the film. *Tabanus* and *Hybomitra* were stuck down at all angles, including head-on. A few *Tabanus* were observed hitting the enclosure at high speed; *Stomoxys* and *Chrysops* were observed landing on the enclosure at low speed. Height distributions were random when a trap was not present inside the enclosure, but small sample sizes limited the power of the tests (*T. quinquevittatus*, 25% low, 44% medium, 31% high; $\chi^2 = 2.1$, d.f. $= 2$; $P = 0.36$, $n = 48$; stable flies, 51% low, 21% medium, 28% high; $\chi^2 = 5.5$, d.f. $= 2$; $P = 0.07$, $n = 43$).

Florida

In total, 47 705 stable flies were captured in the Vestergaard Frandsen version of the Nzi trap at the dairy over 372 trap-days of effort, with an average catch of 128 flies/trap/day (January–August). Results are presented briefly, as no bait was effective.

In experiment 11, catches with a low release rate of acetone plus stable fly faeces were not significantly different from catches with acetone alone ($R = 1.2$ [0.9–1.6], $GM_C = 51$, $F = 1.3$, d.f. $= 1, 26$; $P = 0.27$). In experiment 12, catches with a low release rate of acetone plus faeces were not significantly different from those in an unbaited trap ($R = 1.25$ [0.84–1.86],

Table 3. Catches of *Tabanus quinquevittatus* and *Stomoxys calcitrans* on a transparent triangular sticky enclosure with or without octenol or a Nzi trap present, compared with catches in a similarly baited Nzi trap, and catches in Nzi traps before and after (experiment 10, Ontario).

Afternoon weather*					Experimental conditions		Fly catches	
Day	Main conditions	Wind direction	Speed (km/h)	Temp (° C)	Octenol	Nzi trap	Sticky enclosure	Control Nzi trap
Tabanus quinquevittatus								
1	Sun	W	13.6	28.9	+	+	166	17
3	Sun	WNW	24.0	26.6	+	+	92	1
6	Sun	NNW	15.9	24.3	+	–	36	8
2	Cloud	W	9.1	26.3	–	+	36	0
4	Cloud	NNW	24.6	19.1	–	+	3	0
5	Sun	NNW	18.9	22.6	–	–	12	0
Stomoxys calcitrans								
1	Sun	W	13.6	28.9	+	+	257	10
3	Sun	WNW	24.0	26.6	+	+	251	24
6	Sun	NNW	15.9	24.3	+	–	22	11
2	Cloud	W	9.1	26.3	–	+	97	42
4	Cloud	NNW	24.6	19.1	–	+	48	1
5	Sun	NNW	18.9	22.6	–	–	21	7

Catches 6 days before and 6 days after in Nzi traps†

		Tabanus quinquevittatus	*Stomoxys calcitrans*	*Chrysops*
Before	Octenol	14.5 ± 12.9	7.2 ± 12.9	25.7 ± 23.7
	Unbaited	4.5 ± 6.0	3.5 ± 8.0	16.0 ± 16.5
After	Octenol	5.7 ± 8.2	7.0 ± 14.3	19.5 ± 17.9
	Unbaited	1.5 ± 2.8	1.2 ± 1.5	10.2 ± 12.5

*Means calculated from hourly weather observations from 12.00 hours to 18.00 hours (Environment Canada).
†Mean ± standard deviation ($n = 6$), subset of data from experiment 4.

$GM_C = 40$, $t = 1.14$, d.f. = 36; $P = 0.26$). In experiment 13, catches with a low release rate of acetone plus octenol were not significantly different from those in unbaited traps (pooled for both trap types, $R = 0.95$ [0.44–2.03], $P = 0.9$). Vavoua traps caught significantly fewer stable flies than Nzi traps ($R = 0.43$ [0.21–0.93], $GM_C = 18.5$, $F = 5.0$, d.f. = 1, 33; $P = 0.03$). In experiment 14, retesting faeces with acetone at a higher release rate, catch differences among treatments were not significant ($F = 1.1$, d.f. = 3, 42; $P = 0.36$, $GM_C = 166$). Catches with a simulated heartbeat were equal to those of an unbaited trap ($R = 1.00$ [0.7–1.4]). In experiment 15, testing high release rates of acetone and/or 4MP, differences between treatments were not significant ($F = 0.6$, d.f. = 3, 102; $P = 0.61$, $GM_C = 88$).

Discussion

Attractants

In Canada, octenol increased the catch in Nzi traps of several tabanid species such as *Tabanus similis* Macquart, *T. quinquevittatus*, *Hybomitra lasiophthalma* (Macquart), *Chrysops univittatus* Macquart, and *C. aberrans*, as well as the stable fly *S. calcitrans*. Catches were not improved further when octenol was combined with phenols, or when octenol was combined with phenols plus acetone at either 80 mg/h or 560 mg/h. Acetone alone at 2700 mg/h was not effective. Lastly, aged human urine was not an effective substitute for aged cattle urine. When tested in the U.S.A. for stable flies only, acetone was not effective at 80 mg/h or 250 mg/h alone, or in combination with octenol or stable fly faeces. By contrast, acetone at 890 mg/h was effective in Ethiopia for three *Stomoxys* species, including *S. calcitrans*, but only when used on its own.

A significant increase in catch of *S. calcitrans* with acetone at 62 mg/h vs. unbaited traps was found with sticky traps in Florida, but not at 294 mg/h (Cilek, 1999). Tests with Vavoua traps in Kenya did not find any significant difference in catch with acetone at 880 mg/h, or acetone plus cattle urine, relative to unbaited traps for a *Stomoxys* community dominated by species other than *S. calcitrans* (Mihok *et al.*, 1995). In further tests of acetone (2500 mg/h or 880 mg/h) relative to cattle or rhinoceros urine at two other locations in Kenya, no significant effects on catches of *Stomoxys* spp. were found (Mihok *et al.*, 1996a). Thus, acetone may be useful for increasing catches of *Stomoxys* under certain conditions or release rates, but the nature of these conditions is not clear.

Our inability to adapt standard bait formulations to a new trap application is similar to the results of others who tested baits for biting flies (reviewed by Gibson & Torr, 1999). For example, large increases in the catch of *Tabanus* spp. in F3 traps in Zimbabwe were obtained with several formulations that contain octenol, with or without 4MP and 3PP. Up to a 10-fold increase

Table 4. Distribution of catches of *Tabanus quinquevittatus* and *Stomoxys calcitrans* on the three sides of the transparent sticky enclosure relative to an even distribution (experiment 10, Ontario).

Conditions		Side of sticky enclosure				Statistics	
Octenol	Nzi trap	East	NW	SW	Sample size	χ^2, d.f. = 2	Probability
Tabanus quinquevittatus							
+	+	43%	22%	35%	258	15.9	< 0.001
–	+	28%	26%	46%	39	2.2	0.33
+	–	31%	19%	50%	36	4.2	0.12
–	–	33%	42%	25%	12	–	–
Distribution by collection time with octenol and a trap both present (days 1 and 3)							
09.00 hours		36%	29%	36%	28	0.1	0.96
12.00 hours		39%	21%	40%	57	3.2	0.20
15.00 hours		42%	25%	33%	73	3.0	0.23
18.00 hours		47%	19%	34%	91	10.3	< 0.01
21.00 hours		56%	33%	11%	9	–	–
Stomoxys calcitrans							
+	+	45%	19%	35%	508	50.1	<< 0.001
–	+	28%	35%	37%	145	1.4	0.49
+	–	23%	9%	68%	22	–	–
–	–	24%	33%	43%	21	–	–
Distribution by collection time with octenol and a trap both present (days 1 and 3)							
09.00 hours		86%	0%	14%	7	–	–
12.00 hours		36%	42%	22%	59	3.2	0.21
15.00 hours		42%	18%	40%	138	13.6	< 0.002
18.00 hours		50%	15%	35%	261	47.8	< 0.001
21.00 hours		30%	23%	47%	43	2.9	0.23

in catch occurred with the classic 1 : 4 : 8 formulation (Phelps & Holloway, 1992). A test of the same formulation with canopy traps in Louisiana provided no evidence of synergistic octenol/phenol effects for *Tabanus* spp.; catches were simply increased two-fold as a function of the presence of octenol (Foil & Hribar, 1995). By contrast, experiments with the same canopy trap in Croatia found up to a 51-fold higher catch of several tabanids with baits consisting of aged animal urines (Krčmar *et al.*, 2005, 2006). Further study of the attraction of tabanids to aged urine and its constituent phenols is clearly warranted.

Unlike acetone and phenols, there is considerable evidence for the effectiveness of octenol as a generic bait for many biting insects. There are, however, several differences in efficacy among groups and species (Gibson & Torr, 1999; IAEA, 2003). Some recent results for the efficacy of octenol are a 1.8-fold increase for *Tabanus nigrovittatus* Macquart in box traps with octenol at 3 mg/h (Hayes *et al.*, 1993), a 4.2-fold increase for *Haematopota pluvialis* L. in canopy traps at a low, unmeasured rate (Kristensen & Sommer, 2000), a 9.2-fold increase for *Hybomitra lundbecki* Lynenborg in Malaise traps at 40 mg/h (Nilssen, 1998), and a 7.7-fold increase for tabanids in canopy traps at a high, unmeasured rate (Krčmar *et al.*, 2005). Here, octenol at 1–1.5 mg/h increased the catch of several species up to 2.1 times in traps in Africa and North America, and up to 3.6 times on sticky enclosures surrounding traps in Canada.

Unlike tabanids and tsetse (Gibson & Torr, 1999), there are several key studies where catches of *Stomoxys* spp. have not been increased by baiting traps with octenol, including two experiments reported here. Differential responses to the two stereoisomers could account for inconsistent results, but this is unlikely, given the common use of racemic octenol (Ujváry *et al.*, 2002). The quality of different sources of octenol is also not likely an issue. For example, in our test in Ethiopia with an economical formulation (86% purity), catches of two tsetse species increased, although *Stomoxys* catches did not, providing an internal control. Minor differences among species in attraction could also account for inconsistent results (Mihok *et al.*, 2006). However, this is unlikely, given the predominance of *S. n. niger* and *S. calcitrans* in most African studies. The only consistent factors that stand out when octenol is ineffective are the presence of livestock in the immediate environment, or the use of combination baits. These are reviewed in detail for *Stomoxys* spp. below.

Here, using the same formulation (Dragonfly® lure), octenol increased Nzi trap catches of *S. calcitrans* at a residence in Ontario in the absence of livestock, but did not increase catches at a dairy farm with cattle present at or near trap sites (Florida, with acetone also in the bait). In Ethiopia, a well-replicated test with many bait combinations did not detect any effect of octenol on Nzi trap catches of three *Stomoxys* species. Cattle were

grazing among the trap sites in this test. In Kenya, catches were not affected by octenol at 0.2, 2, 4 or 6 mg/h in Vavoua traps set next to livestock in an urban setting (Mihok *et al.*, 1995). By contrast, octenol at 0.2, 2 or 6 mg/h was about as effective as CO_2 at 2 L/min in experiments set in a nearby national park (Mihok *et al.*, 1995, 1996b). In the same park, octenol was ineffective at 0.3 mg/h in combination with acetone and cattle urine (Mihok *et al.*, 1995). At Nguruman, Kenya, inclusion of octenol at 1 mg/h in combination with cattle or rhinoceros urine and acetone did not affect catches in Vavoua traps (Mihok *et al.*, 1996a). In Mauritius, octenol at 0.5 mg/h was ineffective when Nzi traps were set where farmed deer aggregated (Abeeluck *et al.*, 2001). In Zimbabwe, octenol at 0.6 mg/h was effective on its own with F3 traps at a site remote from livestock, but was not effective in combination with phenols (Holloway & Phelps, 1991). In Mali, the IAEA (2003) noted that catches of *Stomoxys* in 'substantial numbers' were increased 2.9 times in monoconical traps baited with octenol, but did not report the data. This observation is consistent with two-fold higher catches of *Stomoxys* in Mali in pyramidal and Vavoua traps baited with several formulations containing octenol (Djiteye *et al.*, 1998). The main exception to this overall pattern is Cilek (1999). He tested octenol far from livestock and found a significant increase in catch in only one of six tests. He used a very high release rate (18.2 mg/h), which may have been repellent, given results with tsetse (Vale & Hall, 1985). The study by Cilek (1999) was also conducted on a windy beach, where odour cues may have been difficult to detect (Mohamed-Ahmed & Mihok, 1999).

Behaviour

Useful insights into the factors underlying the behavioural responses of tabanids and tsetse to baited artificial objects are scarce in comparison with those available for tsetse (Gibson & Torr, 1999). For savannah tsetse, octenol and acetone increase responsiveness by inducing upwind flight to visually attractive objects (Torr, 1990). Upwind orientation is, however, very imprecise in the absence of CO_2 (Torr & Mangwiro, 1996). Landing behaviour also appears to depend on the presence of CO_2 (Green, 1993). Moreover, species and group differences among tsetse can be critical. For example, many *G. morsitans* will land on a small black cylinder in the absence of a bait, but to attract and induce landing in *G. pallidipes* requires a large object and appropriate attractants (Hargrove, 1980).

The detailed behaviour of biting flies other than tsetse at baited objects has primarily been studied in Zimbabwe, especially in terms of responses to CO_2 (Hargrove & Vale, 1978; Vale, 1980, 1983). For *Tabanus* and Muscidae (unidentified Stomoxyinae and non-biting muscids), baits appear to be effective over short distances, such as in the order of 10–20 m (Vale & Phelps, 1974; Phelps & Vale, 1976; Vale, 1984; McElligott & McIver, 1987). How tabanids and stable flies approach, circle, land on and enter traps in response to visual and olfactory cues has hardly been examined (Vale, 1982a). Video recordings of field behaviour (Brady & Griffiths, 1993) have not been made, although one relevant study has been conducted in the laboratory (Schofield & Brady, 1997). In a wind tunnel, *S. calcitrans* orientated upwind to octenol and acetone, but orientation was not as pronounced as for CO_2. Directed upwind behaviour was reduced at octenol concentrations above 0.02 μg/L; a level similar to natural odour, the 0.01 mg/h exhaled by an ox (Torr *et al.*, 1995). A downwind bias occurred at high concentration, indicating repellency (Schofield & Brady, 1997). These laboratory results conflict with the fact that octenol release rates in field studies (e.g. 1 mg/h or 100 times natural ox odour) are effective attractants (Gibson & Torr, 1999; IAEA, 2003).

To understand differences in trap orientation behaviour among groups of flies, we conducted a few basic experiments with electric nets and sticky enclosures under different bait conditions. These studies revealed multiple and complex differences in responses to artificial objects among *Glossina* and several other genera in the presence and absence of baits. As in previous studies of tsetse only, we found problems in the interpretation of trap efficiency estimates for all groups of flies, as measured by outside vs. inside electric net catches. Anomalies in electric net catch ratios occurred at a considerable distance from traps (6 m vs. a maximum of 4.8 m in Dransfield & Brightwell, 2001). Whether these anomalies were simply the result of flies reacting to 'invisible' electric nets, or were due to the inappropriateness of the 'single-approach' model of fly behaviour, is not clear (Dransfield & Brightwell, 2001).

The use of a sticky enclosure to monitor fly behaviour, with or without a visual target inside (a trap), was only partially informative. As with 'transparent' electric nets (Griffiths & Brady, 1994), certain flies reacted to nominally 'invisible' adhesive film, possibly due to the ultraviolet-absorbing properties of the Rentokil product (see graph, IAEA, 2003, p. 45). In particular, large numbers of *S. niger* were caught on an unbaited sticky enclosure relative to catches in Nzi traps. Catches of *S. calcitrans* and *T. quinquevittatus* on an unbaited sticky enclosure in Canada were also higher than expected in the absence of a substantial visual cue. By contrast, few *Chrysops* and *Glossina* were captured on either an unbaited or an octenol-baited sticky enclosure. These results can be compared with the capture of no *S. calcitrans* on an 'invisible' sticky trap made from adhesive film that does not absorb ultraviolet light (octenol-baited Olson Products sticky sleeve plus small wire frame in Mihok *et al.*, 2006). Altogether, both attraction to and avoidance of Rentokil adhesive film by different species likely contributed to these patterns, confounding a simple interpretation of relative catches on baited vs. unbaited enclosures. Results from sticky catches nevertheless provided useful insights into the optimization of the Nzi trap format for temperate species. Several differences in behaviour among *Tabanus*, *Stomoxys* and *Chrysops* were found (landing on blue or black fabric vs. netting, non-random landing on different surfaces throughout the day, different approach heights and focus on the trap entrance). These could be exploited for targeting specific fauna, as in the complex multiple entrance modification of the Nzi trap (the 'tetra' trap; Dia *et al.*, 2004). Similarly, based on comparisons of traps set facing east or west, and the daily pattern of landing behaviour on trap surfaces, we recommend that traps be set facing the afternoon sun, rather than being set facing downwind, regardless of whether traps are baited or not.

Practical applications

Exploiting practical baits to attract and capture tabanids and stable flies as efficiently as tsetse will require more sophisticated and properly replicated experiments to better understand which behaviours at traps are affected by the presence of baits (Torr & Mangwiro, 1996). Direct video observation in particular should be attempted to sort out artefacts of field techniques (Brady & Griffiths, 1993; Griffiths & Brady, 1994). Replication of studies in behavioural and chemical ecology for biting flies other than tsetse would be valuable to determine why tests of well studied baits and/or traps in new environments produce inconsistent results. This occurs with tsetse (IAEA, 2003), and was found in our experiments in terms of the efficacy of acetone rather than octenol for *Stomoxys* in Ethiopia, and the lack of synergistic effects for AUO for high-altitude populations of tsetse in Ethiopia (Slingenbergh, 1992; Belete *et al.*, 2004).

The ultimate application of field trials of baited traps is the development of economical 'attract-and-kill' systems that are both attractive and efficient. Nzi traps provide a useful option for practical applications in that they catch a broad spectrum of biting insects in both tropical and temperate environments, i.e. they appear to be generally attractive (Mihok, 2002; Mihok *et al.*, 2006). As is shown with electric nets, their efficiency for several biting flies is comparable with that of similar blue-black cloth traps used for tsetse control ('NGU' series, Brightwell *et al.*, 1991; Dransfield & Brightwell, 2001). Specifically, for 'incomplete ring of nets' configurations, and for the same calculation using an electrocution efficiency of 75%, we found a trap efficiency of 25% (males) and 17% (females) for *G. pallidipes* in AUO-baited Nzi traps (6-m ring); vs. 18% (males) and 5% (females) for AUO-baited NG2G traps (4.8-m ring), vs. 36% (males) and 20% (females) for AU-baited NG2B traps (3.3-m ring) (Dransfield & Brightwell, 2001). Efficiency estimates for baited traps in Dransfield & Brightwell (2001) were affected by time of day (our trials were conducted over the entire day), and were highest when nets were placed very close to traps. For example, when an AUO-baited NG2G trap was enclosed in a nearly complete ring of nets at a very short distance (10–40 cm), similar to the sticky enclosure in Canada, trap efficiency for *G. pallidipes* was 58% (males) and 37% (females). Limited comparisons can also be made for *G. longipennis*, which is caught in greater numbers in Nzi than in NG2G traps (Mihok, 2002). Efficiency for this species for Nzi traps (16% pooled average; Table 2) was higher than for NG2B traps (5–11% by three calculation methods; Kyorku *et al.*, 1990).

Comparative estimates of the efficiency of traps in common use for biting flies other than tsetse are not available. For two *S. niger* subspecies, the efficiency of Nzi traps appears to be comparable with that for *G. pallidipes* (Table 2), consistent with improved catches of *Stomoxys* relative to many other traps (Mihok, 2002; Mihok *et al.*, 2006). By comparison, the efficiency of an unbaited biconical trap for Stomoxyinae (*Stomoxys* and *Haematobosca* Bezzi) was estimated at 3–17% in Kenya (Mohamed-Ahmed & Mihok, 1999). These values were from a 'flanking-nets' design. Use of a similar net configuration also provided a low estimate of 6% efficiency for a 'beta trap' for Stomoxyinae (not identified) in Zimbabwe (Vale, 1982b). Use of an 'incomplete-ring design' with an 'A7C trap' baited with the odours emanating from 13 000 kg of livestock provided an efficiency estimate of 13% at the same location (Vale & Hargrove, 1979). For tabanids, data on the efficiency of the Nzi trap have yet to be published; efficiencies of 1–11% were reported for the 'A7C' trap in Zimbabwe (Vale & Hargrove, 1979).

In terms of the overall objective to explore how bait technologies developed in the tropics can be adapted to use in temperate environments, Nzi traps have been shown to be useful for sampling tabanids and stable flies in applied settings, both here and in Mihok *et al.* (2006). Given further refinement of baits and/or trap formats for key pests, phthalogen blue-black traps like the Nzi could provide an environment-friendly option for biting fly suppression (i.e. a 'catch-only' strategy). Biting flies have also been shown to land on the outside surfaces of Nzi traps in large numbers (here and in Mihok *et al.*, 2006). Hence, without further refinement of baits or visual cues, there is potential for the use of traps impregnated with residual insecticides as both killing and capturing devices. This strategy has been facilitated by studies of insecticide-impregnated cloth targets with tsetse in Africa (Mangwiro *et al.*, 1999). Similar studies of the efficacy of cloth targets are also underway in North America (Foil & Younger, 2006; Geden, 2006).

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