

Responses of *Glossina fuscipes fuscipes* (Diptera: Glossinidae) and other Diptera to carbon dioxide in linear and dense forests

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Abstract

The responses of *Glossina fuscipes fuscipes* Newstead and other Diptera to carbon dioxide were studied in linear and dense forests along the shores of Lake Victoria, Kenya. Flies were caught in biconical traps and were intercepted with electric nets while in flight near traps. Carbon dioxide dispensed at a high rate (5 l min^{-1}) in linear forest failed to increase the numbers of tsetse attracted to or caught in traps. In contrast, catches of non-biting Muscidae, Stomoxyinae and Tabanidae were improved by up to 11 times. Inside dense forest, carbon dioxide released at half this rate increased both the numbers of female tsetse attracted to a trap and the catches in a trap by about 2–3 times. Catches of male tsetse were, however, not affected. Striking improvements for other Diptera were also realized (up to 102 times). Under a variety of conditions, unbaited biconical traps attracted many Diptera to the vicinity of a trap, but caught few flies due to low capture efficiencies (typically less than 10%). In contrast, efficiency estimates for *G. f. fuscipes* were good, varying from 37 to 82% in different habitats and seasons. These results are discussed in relation to the search for practical odour attractants for riverine tsetse.

Introduction

Riverine tsetse flies (the *palpalis* group of *Glossina* spp. (Diptera: Glossinidae)) live mostly in dense thickets and forests near water, in contrast to the savannah species (*morsitans* group) which live in much drier and more open habitats (Buxton, 1955). Most of their lives are spent at rest in dense vegetation, with only brief forays into open areas to search for a blood meal. Low metabolic reserves in all tsetse species preclude extensive flight activity (Bursell & Taylor, 1980), and hence, to avoid exhausting reserves, flies must expend energy judiciously. This presents the fly with an energetic dilemma in choosing an appropriate strategy for obtaining blood as well as catering for other activities (Adlington *et al.*, 1996). If it waits for a host to approach its resting site, it will starve within a few days if no host approaches. If it flies too often in search of a host and does

not succeed in feeding, it will exhaust its energy reserves and also starve.

In the dense vegetation typical of riverine tsetse habitats, resting or browsing animals are difficult to locate visually beyond a few metres. Hence riverine tsetse would be expected to preferentially exploit host odour cues to find hosts, whether using a 'sit and wait' or an active searching strategy. Savannah tsetse living in more open habitats rely heavily on odour cues to find hosts, but similar evidence for riverine tsetse is lacking (Green, 1994). Volatiles from host odours induce flies to take off upwind and to exhibit optomotor-steered upwind anemotaxis in flight (Vale, 1984; Brady *et al.*, 1990; Brady & Griffiths, 1993; Torr & Mangwiro, 1996). These behaviours result in successful host location if the odour plume extrapolates upwind towards the host. However, in woody vegetation odour plumes meander in a complex fashion and often result in a confusing or misleading directional signal (Brady *et al.*, 1989). Together, both vegetation structure and wind speed can greatly affect the nature and quality of the directional information delivered to the fly (Paynter & Brady, 1992; Brady *et al.*, 1995).

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Riverine tsetse live in habitats that differ considerably from the open woodlands where detailed studies on olfactory cues and host location in savannah tsetse have been conducted. Their natural habitats are linear forests bordering rivers or lakes. These habitats are now often small and fragmented, and are bordered by extensive cultivated land or pastures. Proximity to large water bodies also has a profound influence on airflow in these natural and disturbed habitats. During the day, land absorbs heat through insolation faster than water. As the air on land warms by convection, a local differential in atmospheric pressure is established. This daily cycle drives wind from water to land at peak tsetse activity. Odour cues from hosts in these habitats are presumably dispersed by high winds constantly towards open habitats, where few if any tsetse are present. In these linear habitats flies may actually have few opportunities to locate hosts through wind-borne odour. Conversely, in larger, dense forests typical of where riverine tsetse evolved, flies presumably intercept odour cues on a regular basis. So long as directionality is not grossly corrupted by vegetation, flies will be guided to the odour source, mainly by upwind anemotactic flight (Colvin & Gibson, 1992). Based on the above, we propose that riverine tsetse such as *Glossina fuscipes fuscipes* Newstead (Diptera: Glossinidae) inhabiting linear habitats with high winds should not respond to artificial baits in the same way as their counterparts in the dense forests.

To test this hypothesis, we conducted experiments on the responses of *G. f. fuscipes* and other Diptera to a presumed universal odour attractant (carbon dioxide) in contrasting habitats along the shores of Lake Victoria, Kenya. Tabanidae, Stomoxyinae and non-biting Muscidae were also studied because of their known attraction to carbon dioxide (Vale, 1980). Insects were caught or intercepted while in flight using blue biconical traps (Challier *et al.*, 1977) and electric nets respectively (Vale, 1974). Here, we report a fundamental difference in the responses of many flies to artificial baits in different vegetation types and discuss the consequences for the development of practical odour baits for riverine tsetse.

Materials and methods

Study sites

The study was conducted between October 1996 and May 1997 near the Ungoye Research Site of the International Centre of Insect Physiology and Ecology (ICIPE) on the shore of Lake Victoria, Kenya (Mohamed-Ahmed & Odulaja, 1997). The area has a warm equatorial climate that is moderated by the proximity of the lake. Some rainfall occurs throughout the year, but there are two times of heavier than normal precipitation: long, from April to June and short from late October to November. Except for a relict, dense natural forest (c. 140 ha), farming has reduced the original lakeshore vegetation to linear forest/thicket patches bordered by open cultivated land. These patches are about 3–10 m high, 5–10 m wide and up to 300 m long. They are dominated by the trees *Sesbania sesban* (Fabaceae) and *Ficus* spp. (Moraceae), usually with a dense understorey of the shrub *Lantana camara* (Verbenaceae), as well as numerous climbers. The Ungoye forest is dominated by *S. sesban* on the shoreline and *Acacia* spp. (Fabaceae), *Combretum* spp. (Combretaceae), *Ficus* spp. and *L. camara* further inland. It contains distinct upper and lower canopies about 20 and 5 m

high with boles up to 100 cm in diameter. Only one tsetse species, *G. f. fuscipes*, occurs in the area at apparent densities of up to a few hundred flies per trap per day. Flies feed mainly on monitor lizards in both vegetation types (Mohamed-Ahmed & Odulaja, 1997).

Catching devices

Tsetse and other Diptera were caught with blue biconical traps or intercepted while in flight with 1.5×1.5 m electric nets (Bonar Industries, Zimbabwe). Electrocutted flies were retained on dull corrugated iron sheets covered with polybutene or shallow trays containing soapy water placed at the base of the nets.

Experiments

Effect of carbon dioxide on attraction to traps

A 300-m linear forest patch near Ngeri Village about 3 km north of the Ungoye forest was used for all experiments. In October 1996 (dry cool period), two traps were placed 100 m apart at sites S1 and S2, about 1 m from the forest edge. Each trap was flanked by two electric nets (fig. 1) to electrocute insects milling about the trap (Vale *et al.*, 1986). One trap was baited with carbon dioxide released from a concealed cylinder at 5 l min^{-1} with the other left unbaited as a control. The control and baited treatments were alternated between the two sites daily for eight consecutive days. The experiment was repeated twice inside the dense forest in March (dry hot period) and May 1997 (wet cool period) using two fixed sites separated by 150 m. Each trap was placed at the centre of a 4-m clearing which had no upper canopy, and hence no shade fell on the trap during experiments. The traps were invisible outside the clearings. In the dense forest, carbon dioxide was released at 2.5 l min^{-1} , i.e. half the rate used in the linear forest. A lower rate was used so that there would be less chance of making a false interpretation of a positive trap response to carbon dioxide in the dense forest.

Effect of carbon dioxide on trap catches

In October 1996, three traps were placed at S1 and S2 and S3 in the linear forest. S3 was 200 m from S2 at the edge of a tiny thicket (c. 10×3 m) near a clearing used by villagers as a fishing dock. The thicket was enclosed from the east and northeast by a high cliff (c. 15 m) with dangling short vegetation. One of the traps was set with two electric nets as described in experiment 1. The second and third traps were used without nets, but one was baited with carbon dioxide at 5 l min^{-1} and the other left unbaited as a control. The treatments were alternated daily between the three sites for nine consecutive days. The experiment was repeated inside the dense forest in March and May 1997 using three sites spaced at 80–100 m with carbon dioxide again released at half the rate used in the linear forest (2.5 l min^{-1}).

Wind characteristics during experiments

Wind direction and speed at 1 m above ground were monitored in the second series of experiments in October 1996 and May 1997. Inside the dense forest, wind direction was recorded daily at 5 min intervals from a 60-cm piece of a

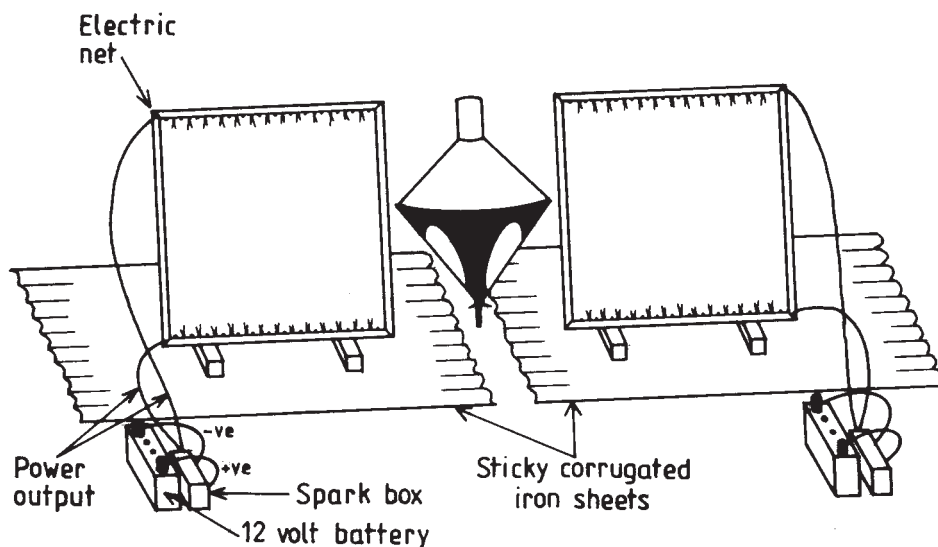


Fig. 1. Biconical trap flanked by two 1.5×1.5 m electric nets used to catch tsetse milling about the trap.

cassette tape fixed to a horizontal branch of a tree, 150 m from the nearest trap site. At the linear forest, records were taken at each of the three sites simultaneously by fixing a tape to thin wooden poles or a tree branch about 2 m from the trap. Observers standing about 30 m to the side of each trap recorded the direction every 5 min. Directions were recorded only to the nearest 45 degrees, thus giving eight possible values: N, NE, E, SE, S, SW, W, NW. With the exception of west, all other directions indicate that wind was blowing from lake to land, i.e. away from the vegetation harbouring tsetse. Wind speed (m s^{-1}) was measured at a single fixed post at each vegetation type using a mini-anemometer accurate to 0.1 m s^{-1} (Testo Term, Germany).

Experimental designs and data analyses

Randomized Latin square designs incorporating the effects of treatments, sites and days were used. Catches were made from 1100 to 1600 h each day, and were transformed to $\log_{10}(n + 1)$ for analysis of variance. Means were separated using the Student-Newman-Keuls (SNK) test at $P < 0.05$. The back-transformed mean treatment catch divided by the back-transformed mean control catch was used as a catch index.

Results

Wind direction

Wind directions for the site in the dense forest and each of the three sites at the linear forest were pooled across days and are presented as percentages in fig. 2. Wind directions between 1100 and 1600 h in these representative dry and wet season samples were predominantly N, NW and NE. Thus wind was blowing from lake to land throughout most experiments. This means that carbon dioxide dispensed at the edge of the linear forest was carried away towards cultivated land. Conversely, inside the dense forest, the plume was moved further inside the forest. The frequency distribution of wind directions differed significantly between sites on most days ($\chi^2 = 13-60$, $P \ll 0.001$),

precluding further generalizations. Average wind speed was $2.7 \pm 0.8 \text{ m s}^{-1}$ (range, 2.1–5) in the linear forest and $0.9 \pm 0.2 \text{ m s}^{-1}$ (range 0.7–1.5) in the dense forest.

Attraction to carbon dioxide

The total of the catch in the biconical trap plus the flies electrocuted by the two adjacent electric nets was used to estimate the number of flies attracted to the vicinity of the trap (Vale *et al.*, 1986). The results in linear forest in the dry season in the first trial revealed similar numbers of male and female *G. f. fuscipes*, Stomoxyinae and non-biting Muscidae attracted to baited versus unbaited traps (back-transformed mean catches of *G. f. fuscipes* for baited/unbaited were 39/32; Stomoxyinae, 47/48; non-biting muscids, 274/268, all statistical tests not significant). However, catches of tabanids (mainly *Tabanus gratus* Loew (Diptera: Tabanidae)) increased significantly (baited/unbaited catches of 7/3).

In the later trials in dense forest, carbon dioxide at half the release rate increased the numbers of female *G. f. fuscipes* attracted to the trap during both dry and wet periods (table 1). Roughly twice as many other kinds of flies were attracted to traps when carbon dioxide was used, but statistically significant differences were obtained only for two of five comparisons: non-biting Muscidae in the wet season, and Tabanidae in the dry season.

Effect of carbon dioxide on trap catches

In the first trial conducted in the dry season in linear forest, similar numbers of both sexes of *G. f. fuscipes* were captured in unbaited and baited traps as were attracted to the trap + nets configuration (table 2). In contrast, large significant differences among treatments were found for all other flies. For example, roughly 70 times more non-biting muscids were attracted to the vicinity of an unbaited trap than were actually captured. Addition of carbon dioxide resulted in a more modest increases in catch (11 times). Significant increases in catch were also observed for Stomoxyinae and tabanids.

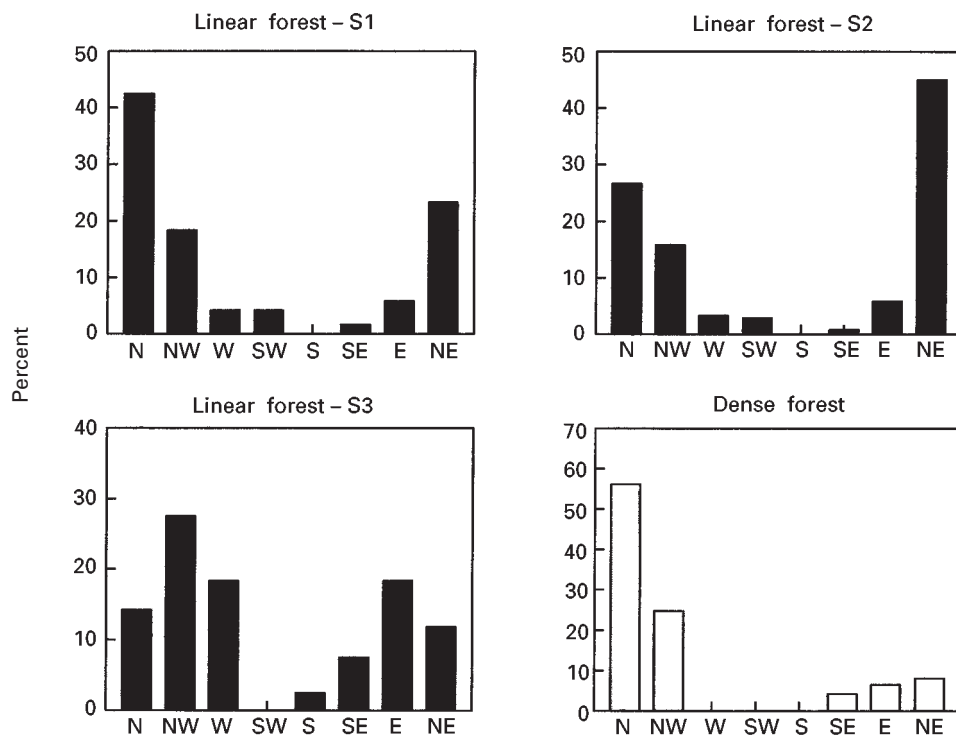


Fig. 2. Wind directions near Ungoye on the shores of Lake Victoria, Kenya at the three sites in the linear forest (■) in October 1996 (dry season) and at one site in the dense forest (□) in May 1997 (wet season).

Table 1. Back-transformed mean catches of *Glossina fuscipes fuscipes* and other biting flies from a biconical trap with two electric nets beside it, baited with or without carbon dioxide released at 2.5 l min^{-1} inside dense forest.

March	Bait	<i>Glossina f. fuscipes</i>				Stomoxiinae (n = 92)		Non-biting Muscidae (n = 1724)		Tabanidae (n = 83)	
		Male (n = 135)		Female (n = 277)		Mean	Index	Mean	Index	Mean	Index
	None	10.5a	1.00	15.1a	1.00	3.7a	1.00	85.1a	1.00	3.6a	1.00
	CO ₂	11.8a	1.12	29.5b	1.95	10.0a	2.68	177.8a	2.09	7.2b	1.99
	F-ratio	0.14		6.66*		3.93		2.76		4.95*	
May		Male (n = 255)		Female (n = 452)		(n = 412)		(n = 1280)			
	None	12.6a	1.00	21.9a	1.00	18.2a	1.00	45.7a	1.00		
	CO ₂	18.3a	1.45	36.3a	1.66	31.6a	1.74	107.2b	2.35		
	F-ratio	2.96		18.00**		3.86		17.79**			

Index = mean treatment catch divided by mean control catch (calculated from back-transformed data).

n, Total caught. Means in the same column with different letters are significantly different ($P < 0.05$) within experiments; * $P < 0.05$, ** $P < 0.001$.

In subsequent trials in dense forest at half the release rate, the catches of female *G. f. fuscipes* in a baited trap were 2–3 times higher than in an unbaited trap in both dry and wet seasons (table 3). Catches in a baited trap were statistically equivalent to the numbers of flies attracted to an unbaited trap. Male catches did not differ among treatments. As in the linear forest, striking differences in catch were found for other flies, especially non-biting muscids. The number of non-biting muscids attracted to an unbaited trap was as much as 102 times greater than the number of flies caught. Traps baited with carbon dioxide caught up to 39 times more flies than unbaited traps.

Trap efficiency

In experiment 2, the design allowed us to calculate the efficiency of an unbaited biconical trap in terms of the number of flies caught relative to the total number of flies attracted to the vicinity of the trap (Vale *et al.*, 1986). For each estimate, we used totals for each replicate in each habitat in each month (i.e. 3-day totals with three sites represented in each total). These estimates were subjected to arcsine transformation and compared by the least significant difference (LSD) test for comparisons among habitats/seasons/sexes.

Table 2. Back-transformed mean catches of *Glossina fuscipes fuscipes* and other biting flies in biconical traps baited with or without carbon dioxide released at 5 l min⁻¹ inside linear forest, compared with the catch in an unbaited biconical trap with two electric nets beside it.

Bait	<i>Glossina f. fuscipes</i>				Stomoxyinae		Non-biting Muscidae		Tabanidae	
	Male (n = 411)		Female (n = 829)		(n = 605)		(n = 4333)		(n = 75)	
	Mean	Index	Mean	Index	Mean	Index	Mean	Index	Mean	Index
Trap	12.0	1.00	18.6	1.00	3.4a	1.00	5.8a	1.00	1.3a	1.00
Trap+CO ₂	14.0	1.18	28.8	1.55	8.5b	2.50	62.6b	10.79	3.3b	2.54
Trap+nets	13.8	1.15	28.2	1.52	44.7c	13.15	408.1c	70.36	5.6bc	4.31
F-ratio	0.20		2.49		56.6**		76.9**		31.5**	

Index = mean treatment catch divided by mean control catch (calculated from back-transformed data).

n, Total caught. Means in the same column with different letters are significantly different ($P < 0.05$) within experiments; * $P < 0.05$, ** $P < 0.001$.

Table 3. Back-transformed mean catches of *Glossina fuscipes fuscipes* and other biting flies in biconical traps baited with or without carbon dioxide released at 2.5 l min⁻¹ inside dense forest, compared with the catch in an unbaited biconical trap with two electric nets beside it.

March	<i>Glossina f. fuscipes</i>				Stomoxyinae		Non-biting Muscidae		Tabanidae	
	Male (n = 181)		Female (n = 285)		(n = 271)		(n = 1614)		(n = 49)	
Bait	Mean	Index	Mean	Index	Mean	Index	Mean	Index	Mean	Index
Trap	7.8a	1.00	7.6a	1.00	1.7a	1.00	1.7a	1.00	1.4a	1.00
Trap+CO ₂	10.6a	1.36	17.4b	2.29	7.6b	4.47	66.1b	38.88	3.5b	2.50
Trap+nets	10.9a	1.39	21.4b	2.81	34.7bc	20.41	173.8bc	102.24	4.2b	3.00
F-ratio	3.34		12.7*		123.70**		224.59**		7.28*	
May	Male (n = 160)		Female (n = 301)		(n = 176)		(n = 536)			
Trap	6.7a	1.00	8.5a	1.00	1.9a	1.00	1.7a	1.00		
Trap+CO ₂	9.1a	1.17	20.4b	2.40	7.6b	4.00	24.0b	14.11		
Trap+nets	10.2a	1.52	20.8b	2.46	20.0bc	10.52	57.5b	33.82		
F-ratio	4.73		12.7*		108.03**		52.71*			

Index = mean treatment catch divided by mean control catch (calculated from back-transformed data).

n, Total caught. Very few tabanids were caught in May. Means in the same column with different letters are significantly different ($P < 0.05$) within experiments; * $P < 0.05$, ** $P < 0.001$.

An unbaited biconical trap caught from 37 to 85% of the *G. f. fuscipes* that approached it in different habitats and seasons (table 4). Efficiency estimates had large standard deviations and therefore showed only very general trends. The only significant result was a higher trap efficiency in the linear forest in October for the total tsetse catch ($P < 0.05$). Trap efficiencies for Stomoxyinae (3–17%), non-biting Muscidae (<3%) and Tabanidae (15–23%) were low and highly variable.

Discussion

Carbon dioxide is a well-established and potent attractant for a large variety of haematophagous Diptera. In the well-studied savannah tsetse species, it doubles catches at visual targets when dispensed at about 2 l min⁻¹ (Vale & Hall, 1985); there is only minimal improvement in catch above this level (Torr, 1990). With other Diptera, much more dramatic increases in catch occur at both high and low release rates. For example, catches of Tabanidae, Stomoxyinae and non-biting Muscidae were increased 7–20 times at 2.5 l min⁻¹ and 38–47 times at 15 l min⁻¹ in extensive electric net experiments with visual targets in Zimbabwe (Vale, 1980). Carbon dioxide can also act synergistically with

Table 4. Mean percent efficiency \pm SD of unbaited biconical traps for *Glossina fuscipes fuscipes* and other Diptera in linear and dense forests.

	Linear forest (October)	Dense forest (March)	Dense forest (May)
<i>Glossina f. fuscipes</i>			
Male	84.6 \pm 9.3	74.4 \pm 36.2	65.6 \pm 26.4
Female	75.8 \pm 12.6	37.3 \pm 9.2	37.1 \pm 12.5
Total	82.3a \pm 14.5	47.3b \pm 2.2	45.5b \pm 13.2
Other flies			
Stomoxyinae	16.7 \pm 22.4	3.0 \pm 0.1	6.0 \pm 0.1
Non-biting Muscidae	2.4 \pm 0.1	0.6 \pm 0.1	1.6 \pm 0.1
Tabanidae	22.5 \pm 27.8	15.0 \pm 21.2	–

Means in the same row associated with different letters are significantly different at $P < 0.05$; –, very few tabanids were caught.

attractants such as acetone and 1-octen-3-ol to produce large increases in catch for tsetse (Torr *et al.*, 1995), and other Diptera (Mihok *et al.*, 1996).

In agreement with the above, we found a 2- to 3-fold increase in the catches of *G. fuscipes* in dense forest at a release rate of 2.5 l min^{-1} . These results were obtained in both wet and dry seasons using two methods for enumerating flies: those caught in traps, and those attracted to a visual target (trap) with adjacent electric nets. For unknown reasons, only females responded to the odour attractant. Male–female differences in trap-oriented behaviour are pronounced in *G. f. fuscipes* (Odulaja & Mohamed-Ahmed, 1997), but we have yet to understand the root causes. Results for other Diptera in dense forest were similar to results obtained by other workers; for example catches were increased by up to 39 times relative to an unbaited trap for non-biting muscids. These very large increases in catch appear to be related to trap efficiency, rather than attraction. Addition of carbon dioxide to the configuration of a trap plus electric nets increased the total numbers of flies attracted by only 2- to 3-fold. Unfortunately, we never ran an experiment to estimate trap efficiency directly in the presence of carbon dioxide. Hence inferences about the effects of carbon dioxide on trap efficiency versus attraction are based only on the magnitude of catches with different configurations of nets and baits across experiments.

As per our original hypothesis, contrasting results were obtained in linear forest. For *G. fuscipes*, two experiments failed to detect any effect of carbon dioxide on either trap catches or the total number of flies attracted to the trap. These experiments were done with reasonable statistical power (catches of 30–40 tsetse per trap per day) at twice the release rate used in the dense forest. Trap catches of other Diptera were, however, increased as expected with carbon dioxide, although not as dramatically as in dense forest. Similarly, in contrast to the 2- to 3-fold increase in dense forest, numbers of other Diptera attracted to the trap were not increased in the presence of odour (with the exception of *Tabanus gratus*). As responses to baits in African Tabanidae (Phelps & Holloway, 1992) and Stomoxyinae (Mihok *et al.*, 1996) are often species-specific, it is best to interpret habitat differences for other Diptera with caution.

The failure of carbon dioxide to either attract *G. fuscipes* to the vicinity of a trap, or to potentiate its capture in the trap itself in linear forest habitat, could be due to any number of factors specific to the microenvironments represented by the two habitats (Griffiths & Brady, 1995). However, we feel that our hypothesis highlighting wind speeds and directions can account for these results in the most straightforward manner. In savannah tsetse, successful location of an odour source depends on the 'straightness' of airflow, which increases, regardless of vegetation type, as the wind speed increases up to about 1 m s^{-1} (Brady *et al.*, 1989). In the present work, wind speeds at times of tsetse activity were nearly always higher than this threshold, both inside the dense forest ($0.7\text{--}1.5 \text{ m s}^{-1}$) and inside the linear forest ($2.1\text{--}5.0 \text{ m s}^{-1}$). These fast winds presumably provided reliable directional information, but at the same time, greatly reduced concentrations of the attractant. Hence, the simplest explanation for our results is that the 'active space' of the plume may have been insufficient to stimulate large numbers of flies in linear forest (which was only 5–10 m wide and surrounded by lake or farmland), whether in flight or at rest (Brady *et al.*, 1995; Torr & Mwangiro, 1996).

Until recently, the *palpalis* group was believed to hunt largely by vision (Laveissière *et al.*, 1990). This interpretation was based on the absence of consistent evidence for increases in catch using odour baits effective for savannah species (Green, 1994). In contrast to the many failures with synthetic baits of bovine origin, catches of riverine species have been increased by using carbon dioxide: *G. tachinoides* Westwood (Galey *et al.*, 1986), *G. f. fuscipes* and *G. f. quazinensis* Pires (Rogers, 1970; Frezil & Carnevale, 1976). For example, Frezil & Carnevale (1976) obtained a 2.8-fold increase in the catch of *G. f. quazinensis* in a small experiment at the Brazzaville Zoo by baiting biconical traps at ten sites on different days with blocks of dry ice. Over a much longer period, trap catches were increased 40-fold from an expected baseline value for an unbaited trap of 0.17 flies per trap per day. *Glossina f. fuscipes* is also attracted to the smell of its main host, the Nile monitor lizard (Gouteux *et al.*, 1995). Unknown compounds within cattle odour and monitor lizard odour (other than carbon dioxide) are attractive to *G. f. fuscipes* (Mohamed-Ahmed, unpublished). These results are contrary to conventional wisdom for riverine tsetse, and are also contrary to earlier detailed studies conducted in our study area (Mwangelwa *et al.*, 1995).

These contradictions suggest that problems of experimental design in 'simple' field trials may be more acute than tsetse researchers have previously thought. For example, we propose that the experiments of Mwangelwa *et al.* (1995) on odour attractants for *G. f. fuscipes* were severely compromised as a result of conducting studies only in linear lakeshore habitats. Similarly, in working with *G. tachinoides* in West Africa, researchers may not have considered the consequences of wind direction and the concentration of flies near water as confounding effects in the layout of critical experiments (Filledier & Merot, 1989; Amsler *et al.*, 1994; Späth, 1995). Altogether, there are numerous examples of negative results, as well as conflicting results when odour trials are conducted in different seasons or geographical areas. Perhaps the classic example comes from trials conducted in Somalia with one of the most-studied species of savannah tsetse, *G. pallidipes* Austen (Torr *et al.*, 1989). Torr and colleagues were unable to replicate the very large increases in catch of *G. pallidipes* seen in other countries with ox odour or its synthetic components. Their study was conducted in an area with high winds ($5\text{--}7 \text{ m s}^{-1}$); experiments were also set in linear dense thicket along the edge of a drainage channel next to open woodland. These features suggest a situation similar to the linear forest at Ungoye. Lastly, these experiments were conducted in the dry season, when tsetse take on a linear distribution near water, e.g. in gallery forest on the banks of the River Shebele (Mohamed-Ahmed & Dairri, 1987).

In conclusion, our work stresses the importance of ecological and behavioural considerations related to host location as key starting points in the design of experiments screening odour attractants. The spatial distribution, searching strategies, wind direction and speed, vegetation structure and type in different seasons, etc. can confound results and lead one to abandon useful attractants. Perhaps because of the above, we have yet to find a practical attractant for riverine tsetse, even though it probably exists. More focused ecological research and better experimental designs are now needed to exploit the recent discoveries of promising attractants from natural hosts such as the monitor lizard.

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