

## Wind speed effects on odour source location by tsetse flies (*Glossina*)

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**Abstract.** Tsetse flies (mainly *Glossina pallidipes* Aust.) were captured by various means at sources of artificial host odour in Zimbabwe and Kenya. Their rates of arrival and flight directions were compared with simultaneous data on the wind's speed and direction, on time-scales ranging from 1 s to 30 min. It was predicted that because increasing wind speed up to  $1 \text{ m s}^{-1}$  straightens out the airflow (Brady *et al.*, 1989) it will straighten out odour plumes, make them easier to navigate, and should therefore increase the rate of arrival of flies at an odour source. In the event, the relationship proved to be more complex, with both positive and negative correlations of arrival rate on wind speed. It seems there is a bimodal relationship: odour source finding is positively related to increasing wind speed in weak winds up to  $\sim 0.5 \text{ m s}^{-1}$  (presumably as the odour plume straightens out), but is negatively related to increasing wind speed in strong winds above  $\sim 1.0 \text{ m s}^{-1}$  (presumably due to increasing turbulence breaking up the odour plume).

**Key words.** *Glossina*, tsetse fly, behaviour, anemotaxis, flight, orientation, odour plume, wind speed, turbulence.

### Introduction

Many flying insects locate distant invisible sources of 'attractant' odour by using optomotor-steered anemotaxis to fly upwind when in contact with above threshold odour concentrations (Kennedy, 1992, ch. 6.4). Successful location of an odour source by this method of orientation requires that the odour plume shall extrapolate reliably back upwind towards the source (David *et al.*, 1982, 1983; David, 1986). In vegetation, however, this ideal situation is commonly replaced by one in which the odour plume meanders in a highly non-linear manner (Elkinton *et al.*, 1987; Brady *et al.*, 1989, 1990).

The straightness of airflow increases with wind speed up to about  $1 \text{ m s}^{-1}$  (Brady *et al.*, 1989, 1990; Griffiths & Brady, 1995). Odour plumes in vegetation, where the wind is commonly less than  $0.5 \text{ m s}^{-1}$ , should therefore drift straighter as the wind increases. This should encourage insects' anemotactic responses to lead them upwind more directly to the odour source as the wind speeds up. Conversely, as the wind slows down towards its typical speeds in thick vegetation, it may meander so much that odour plumes actually turn back on themselves (*loc. cit.*). Flying upwind then will lead the insect away from the source. It might therefore be predicted that tsetse flies, and other insects hunting odour sources anemotactically, would find it easier to do so in faster winds than in slow. This general hypothesis is over-simplistic for several reasons, however.

First, although faster winds do create straighter odour plumes, such plumes are more dilute than plumes created in weaker winds, because a given initial amount of odour is entrained into a greater volume of passing air. In the Sutton and other Gaussian models, dispersion is an inverse function of wind speed, indicating greater dilution from the greater turbulence in higher winds, and hence a smaller above threshold 'active space' of the plume (even though the average flux of odour molecules may be unchanged; and cf. Griffiths & Brady, 1995, Fig. 4). [This subject is excellently reviewed by Elkinton & Cardé (1984) and Murlis *et al.* (1992).]

Second, although plumes in weak winds will travel less far (for a given concentration isopleth), they will be swung more to and fro across the bush and thus be wider, potentially sweeping a greater area at above threshold concentration. More insects may therefore be stimulated by the odour in slow winds than in fast – and there is evidence that more tsetse flies take off spontaneously in weak wind than in strong (Warnes, 1992).

Third, there are complex spatial interactions between odour plume structure and the timing of the flying insect's detection of puffs of above-threshold odour, which may affect its mode of response (Mafra-Neto & Cardé, 1994; Vickers & Baker, 1994). In tsetse there are also interactions between wind-driven anemotactic responses (Gibson *et al.*, 1991) and non-directional orthokinetic or klinokinetic responses to odour (Warnes, 1990; Paynter & Brady, 1993; see Williams, 1994).

Finally, insects will detect odour in two different aerodynamic situations – perched and flying – and the relationship between the wind's movement and the insect's wind-direction receptors is

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radically different in the two (Brady *et al.*, 1989). For the tsetse fly, which spends 99% of its time at rest (Brady, 1972, 1988), odour detection may occur most often when it is perched.

This paper reports several attempts to explore the relationship between wind speed and various measures of tsetse flies' success at finding sources of artificial host odour. The answers turn out to be more complicated than expected.

## Materials and Methods

**Sites.** Observations were carried out at three sites: at Rekomitjie Research Station in the Zambezi valley, northern Zimbabwe (see Vale, 1974; Vale *et al.*, 1988); at the I.C.I.P.E. Field Station at Nguruman, south-western Kenya (see Williams *et al.*, 1990); and in the Shimba Hills near the Kenyan coast. All are areas of high tsetse density in typical bush savannah habitat, but the experimental sites differed in detailed appearance (see below). By far the commonest tsetse present was *Glossina pallidipes* Austen, and, with one exception, all the results quoted refer to it alone, although the minor species (*G.m.morsitans* Westwood in Zimbabwe, and *G.longipennis* Corti and *G.brevipalpis* Newstead in Kenya) followed the same trends. Observations were carried out during the peak of *G.pallidipes* activity, between about 15.00 and 18.00 hours local time (except for experiment 8, which lasted all day).

**Fly sampling methods.** Eight experiments were performed to measure the arrival rate, and in some cases also the direction of arrival of tsetse flies; each involved some sort of visual target baited with various forms of synthetic ox odour, with or without CO<sub>2</sub>, and recorded contemporary data on wind speed and direction.

**Experiment 1.** At Rekomitjie, a 1-m<sup>2</sup> black cloth screen with an electric grid on each face (flanked by two electrified 1/2-m<sup>2</sup> mosquito netting screens; see Griffiths & Brady, 1994) was set across the mean wind line, with sticky trays laid out below to catch the stunned flies so that the putatively upwind-approaching and downwind-approaching flies could be separated. It was odour-baited at its foot with a bottle of acetone delivering ~500 mg h<sup>-1</sup>, and a polythene sachet delivering ~0.1, 0.4 and 0.8 mg h<sup>-1</sup> of 3-*n*-propylphenol, 1-octen-3-ol, and 4-methylphenol, respectively. Even in the absence of CO<sub>2</sub> these constitute a reasonable surrogate for ox odour in the sense that the combination 'attracts' large numbers of tsetse flies (Vale *et al.*, 1988), and evokes upwind flight, both in the laboratory (Paynter & Brady, 1993) and in the field (Brady & Griffiths, 1993).

The target was visited to collect and count the caught flies every 10 min; this was done with the power switched off, but even if the movement of the two collectors did attract some flies, that effect would have been constant for all collections. Catches ranged from 0 to 118 per 10 min. Observations were in March 1990, just after the rains, when the bush was in full leaf, but the site was in open 'mopani' woodland with no trees higher than 3.5 m for several tens of metres in all directions; this was chosen deliberately, to keep the plume reasonably straight and orthogonal to the target, by encouraging relatively unimpeded airflow past the target and beyond. The target was visible to the human eye from ~20 m.

**Experiment 2.** At Nguruman, a 1-m<sup>2</sup>, double-sided electric net (the two sides separated by mosquito netting) was set across the mean wind line with catching trays below, as in expt 1. The system was baited visually on its upwind side with a model 'warthog'

(a black drum ~50 cm × 30 cm diam.; Vale, 1974), and was odour baited with a bottle of acetone (delivering ~500 mg h<sup>-1</sup>) and a bottle of 3-month-old ox urine. Again, these provide a functional imitation of ox odour (Dransfield *et al.*, 1986, 1991). Flies were collected every 10 min as in expt 1; the catch ranged from 0 to 71 per 10 min. Observations were done over 3 weeks in the dry season (July–August 1990). The site was among scattered large trees at the edge of gallery forest, but towards the mainly downwind side much of the herbage had been burnt out, and towards the mainly upwind side was open grassland ~1 m tall; as in expt 1, this was chosen to allow a relatively unimpeded wind flow past the target and odour source. The 'warthog' was visible from ~50 m upwind and ~20 m downwind.

**Experiment 3.** At Nguruman, a blue and black 'Ngu-B' trap (roughly 1-m-cubed; Dransfield *et al.*, 1991) was used as a visual bait, with a 1-m<sup>2</sup> electric net placed across its entrance. The odour bait was a broad plume of CO<sub>2</sub> (a good stimulant of upwind flight; see e.g. Colvin *et al.*, 1989) delivered at ~2 l min<sup>-1</sup> from a 3-m-long perforated pipe, plus a bottle of acetone and a bottle of 3-month-old ox urine as in expt 2. An overhead video camera with wide-angle lens (Cohu/Fujinon) recorded the knock-down of flies as they hit the electric net; arrival direction was not measurable in this system. Observations were done over 6 weeks in the dry season (July–August 1990); the site was in dense riverine bush with an overstorey of *Ficus* sp. trees (see Paynter & Brady, 1992), in a ~10-m diameter clearing beyond which the trap was invisible.

**Experiment 4.** At Rekomitjie, a model 'warthog' plus a 1-m<sup>2</sup> electric net (as in expt 2) was sited over a shute that delivered the knocked-down flies to an underground chamber in which an invisible observer identified, timed and recorded the flies as they were caught, separately for the two sides of the electric net. The target was baited with a point source of CO<sub>2</sub>, plus acetone and an octenol/phenols sachet as in expt 1. Marked flies were video-recorded at their release from a site 50 m or 75 m away down the mean wind line. Thus, both the flight duration (to ±1 s) and straight-line distance of flight of the marked flies were known. Sample duration was ~20 min (the duration of a video cassette). About 90% of the flies were caught on the downwind-facing side of the electric net. The observations were part of the work reported in Griffiths *et al.* (1995), and were done in the dry season (August–October 1991), when the vegetation was largely leafless and the herbage mostly grazed flat; the target was visible from 20–30 m.

**Experiment 5.** Within expt 4 at Rekomitjie, the arrival rates of 'wild' unmarked flies that had not been released artificially from known distances were also recorded at the observation chamber. This was done to the nearest 10 s.

**Experiment 6.** At Rekomitjie, a 0.75-m<sup>2</sup> black target was set parallel to the mean wind line, and an overhead video camera (as in expt 3) recorded the arrival, departure and flight directions of flies. The target was odour-baited with three bottles of acetone and three octenol/phenols sachets (see expt 1) arranged in an arc 5 or 10 m away upwind to ensure that the odour plume passed over the visual target at virtually all times. Fly arrival times and flight directions were taken each second from the monitor screen on play-back. The observations were done in the dry season, within the study by Brady & Griffiths (1993), and were contemporary with expt 4. The target was visible ~20–30 m away. As the flies were not killed in this system, some may have left the target and then returned to it, to be recorded more than once. The

amount of this behaviour was not assessable, but should not have seriously biased the results, since experiments with supplementary electric nets around odour sources imply that tsetse do not stay around sources for long (Griffiths *et al.*, 1995), possibly because the upwind area is swept clean of odour by the wind.

**Experiment 7.** At Shimba, a 1-m<sup>2</sup> electric net (as in expt 2) was set across the mean wind line with a 1-m<sup>2</sup> royal blue cloth target placed vertically beside and in line with it to act as visual bait (as in Green, 1990). This was odour baited with CO<sub>2</sub> alone, released at ~2 l min<sup>-1</sup> from a 1-m-long perforated pipe (similar to expt 3). Flies were collected every 10 min over seven afternoons spread through September and October 1992; the catch ranged from 0 to 20 flies per 10 min. The site was in shrubby grassland (grass ~0.5 m high with shrubs covering ~10% of the area) about 50 m from the edge of thick woodland; the target was visible from ~20 m.

**Experiment 8.** Also at Shimba, the same set-up as for expt 7 (baited as in expt 2) was used within an area of shady forest (~30 m in from its edge) in which the target was visible from only ~5 m. The site was on the brow of a hill, however, and so exposed to high afternoon winds (Table 1). Flies were collected every 30 min over 6 days in October–November 1992; catches ranged from 0 to 18 flies per 30 min, and were not separated into upwind and downwind arrivals.

**Wind data.** Wind speed and direction were recorded at each target site continuously during the observations. Two monitoring systems were used: expts 1–3 and 7–8 used sensitive three-cup or six-cup anemometers plus a light mechanical wind-vane (Vector Instruments, Clwyd) coupled to a datalogger (either Squirrel or Delta-T, Newmarket); expts 4–6 used a solid-state ultrasonic anemometer (1012-S, Gill Instruments) that measured wind speed and direction simultaneously (technical details in Griffiths & Brady, 1995). The first system recorded contemporary temperature at the anemometer; for the second system we took maximum temperatures daily from a meteorological station ~1 km away. Both systems recorded the wind on a 1-s sample frequency, but except where indicated the analyses were based on averages of 10-s means. Data on the wind structure during these observations are analysed in Griffiths & Brady (1995).

Since the wind's speed distribution within vegetation is strongly skewed to episodes below 0.5 m s<sup>-1</sup> (Brady *et al.*, 1989), its mean over a succession of minutes may be a largely irrelevant parameter from the flying insect's point of view, if it is mainly the rarer fast episodes which are orientationally usable by the flies. We therefore examined alternative measures, including the variance, standard

deviation and coefficient of variation of the speed, and the percentage of time the wind ran at >0.25, >0.5 and >0.8 m s<sup>-1</sup>. The last measures always correlated closely with the mean speed ( $r^2$  often >90%; Griffiths & Brady, 1995); they also often correlated better with the flies' rate of arrival at an odour source than did the mean.

**Analysis.** The basic statistical approach was to look for simple linear correlations, with the  $x$  and/or  $y$  values variously transformed. More sophisticated analyses of covariance were performed using GLIM (McCullagh & Nelder, 1983; Crawley, 1993) to determine the catch deviance attributable to wind speed, time of day, and temperature. Where the relationship between catch and wind speed (or temperature) appeared to be non-linear, a wind speed squared transformation was included among the variables to test for curvilinear regressions (see Sokal & Rohlf, 1981). A Poisson error distribution (log-link) was also used, and the scale factor adjusted to allow for the data being over-dispersed (Crawley, 1993). Time and other explanatory variables were individually removed from the maximal model and tested for significance ( $\chi^2$ ) by the change in residual deviance. Other techniques are explained where appropriate in the text.

## Results

With eight sets of observations, each with fly arrival rates sampled on several time-scales, and each with up to ten wind parameters, we analysed many scores of potential relationships. We report here only key, representative cases.

### Wind characteristics

Details of the winds in the eight experiments are summarized in Table 1. The overall means were similar in expts 1–7, ranging from 0.47 m s<sup>-1</sup> in the very dense bush of expt 3 to 0.97 m s<sup>-1</sup> in the open, dry-season woodland of expt 6. The hilltop site of expt 8 was windier than the other sites, with a mean of 1.3 m s<sup>-1</sup>, but its range of speeds was not much different from those in expt 2. The mean wind speeds generally reflected the centre of the local wind-speed distribution, since means and medians approximately coincided. The exception was expt 2, which also included the widest range of wind speed variances. Otherwise the winds in the different experiments showed similar speed structures: they had high

Table 1. Details of the mean winds in the six experiments.

Experiment	Overall mean (m s <sup>-1</sup> )	Overall median (m s <sup>-1</sup> )	Range of means (min–max)	Range of SDs (min–max)	SD vs Mean ( $r^2$ )
	0.64	0.61	0.10–1.35	0.05–0.42	52%
2	0.65	0.44	0.06–3.31	0.06–2.44	80%
3	0.47	0.47	0.10–1.06	0.05–0.52	30%
4	0.94	0.90	0.38–1.82	0.01–0.60	94%
5	0.91	0.86	0.29–2.11	0.19–0.90	91%
6	0.97	0.94	0.39–1.63	0.15–0.83	50%
7	0.50	0.53	0.17–0.85	–	–
8	1.30	1.08	0.00–3.50	–	–

**Table 2.** Correlations between the arrival rates of *G.pallidipes* at odour-baited visual targets and the wind speed (positive and negative correlations shown as + or -r<sup>2</sup>%).

Sample duration	r <sup>2</sup> for various wind speed measures			
	Mean speed	% >1/4 or >1/2 m s <sup>-1</sup>	SD mean	
Expt 1: Zimbabwe: electrified vertical target				
10 min	66	+8* <sup>1</sup>	+16*** <sup>1</sup>	
Expt 2: Kenya: 'warthog' with electric net				
10 min	48	+14** <sup>2</sup>	+5 <sup>NS</sup>	
Expt 3: Kenya: 'Ngu' trap with video				
50 s	80	+1 <sup>NS</sup>	<1	+10**
200 s	20	+3 <sup>NS</sup>	+14*	+47***
Expt 4: Zimbabwe: mark-release with electric net				
20 min	24	-11*	-2 <sup>NS</sup>	-3 <sup>NS</sup>
Expt 5: Zimbabwe: 'warthog' with visual recording				
100 s	39	-10*	-9 <sup>NS</sup>	<1
5 min	84	-31***		-30***
Expt 6: Zimbabwe: vertical target with video				
1 min	56	-15**	-11*	-3 <sup>NS</sup>
2 min	28	-24**	-26**	-4 <sup>NS</sup>
Expt 7: Kenya: electrified vertical target (grassland)				
10 min	115	+9** <sup>3</sup>		
Expt 8: Kenya: electrified vertical target (forest)				
30 min	134	+1 <sup>NS</sup> <sup>4</sup>		

*n* = number of time samples. \**P* < 0.05, (\**P* = 0.06, \*\**P* < 0.01, \*\*\**P* < 0.001.

<sup>1</sup> The true relationship with wind speed appears bimodal: for mean wind speeds it is positive up to -0.6 m s<sup>-1</sup> (*r*<sup>2</sup> = +52%\*\*\*), but negative in faster winds (*r*<sup>2</sup> = -11%\*\*), with *r*<sup>2</sup> = 13%\*\* for the overall curvilinear relationship (see Fig. 1A).

<sup>2</sup> This regression done versus log wind speed because of four samples with high mean wind speeds: without these (= same wind range as in expt 1) the regression is non-significant.

<sup>3</sup> This correlation is for the linear regression but, as in expt 1, the relationship is probably bimodal: for the curvilinear relationship *r*<sup>2</sup> = 16%\*\*\* (see Fig. 1B).

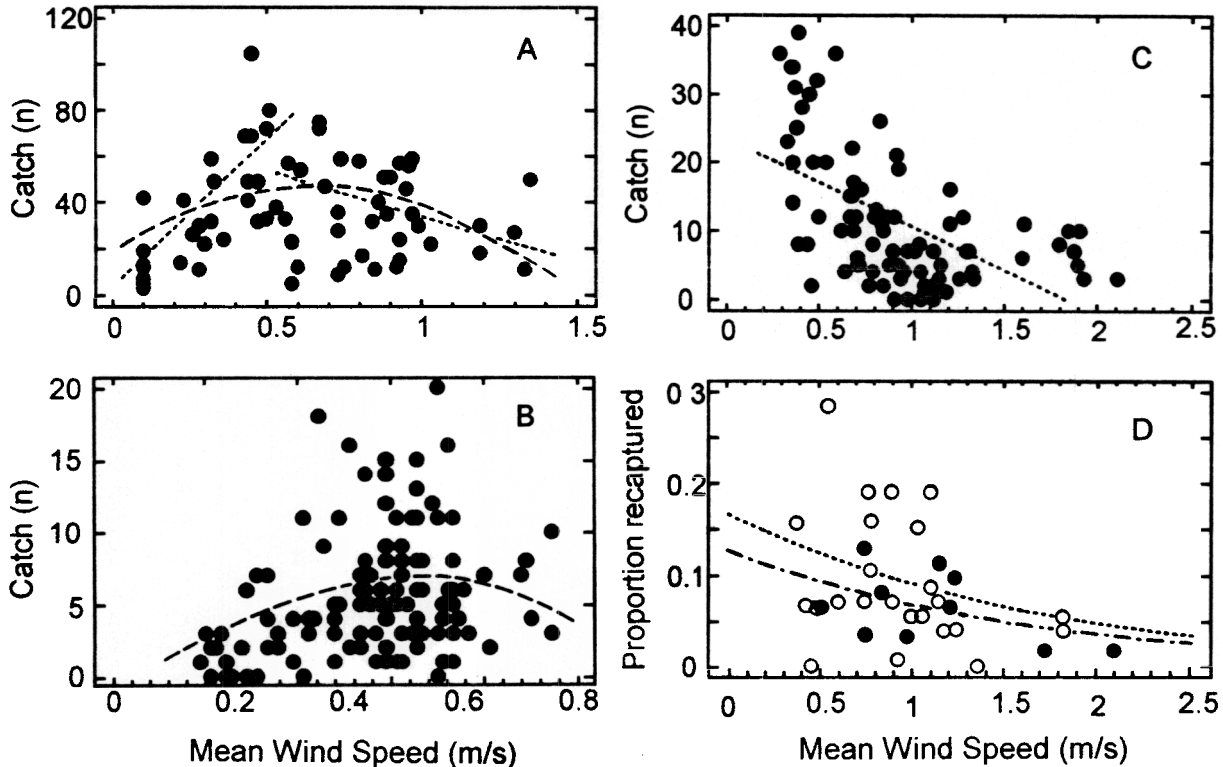
<sup>4</sup> For the curvilinear relationship, *r*<sup>2</sup> = 10%\*\*.

correlations between mean speeds and standard deviations of speed, and their lowest wind episodes were always close to zero m s<sup>-1</sup> (although variance was not recorded in expts 7 and 8).

**Experiment 1: 10-min arrivals at a 1-m<sup>2</sup> black target (Zimbabwe).** Set across the wind line, this was found by the flies roughly in proportion to the wind speed, but the linear correlations, though often significant, explain little of the variance (i.e. *r*<sup>2</sup> < 20%; Table 2). Correlation was significantly better with wind speed expressed as the proportion of it that blew at over 0.5 m s<sup>-1</sup> than expressed as the simple mean speed. However, there is good evidence for the relationship in reality being bimodal: the correlation is strongly positive over the lower half of the wind speed distribution and negative over the upper half (see footnote 1, Table 2). The statistical significance of this bimodality was confirmed by performing multiple regressions on wind speed and wind speed squared which, allowing for both temperature and time of day effects, revealed a significant curvilinear relationship with wind speed (Fig. 1A).

**Experiment 2: 10-min arrivals at a 'warthog' (Kenya).** Flies found the model warthog roughly in proportion to the wind speed (Table 2). However, the significant coefficient of 14% is due almost entirely to four high wind-speed points, without which the correlation disappears (*r*<sup>2</sup> < 1% regardless of how the data are transformed). On the other hand, the correlation with the standard deviation of the wind speed, though also influenced by a few high points, survives when log-transformed to centre these outliers (*r*<sup>2</sup> then +12%\*).

**Experiment 3: videoed arrivals at an 'Ngu' trap (Kenya).** These arrivals were pooled for analysis into 50-s, 100-s, 200-s and 400-s bins. Most of the regressions against wind speed were very weak (Table 2), but this was another situation where there was a stronger correlation with the proportion of the wind that was relatively fast (>0.25 m s<sup>-1</sup>) than with the mean. The arrival rates were unusual in being very highly correlated with the SD of the wind speed (up to *r*<sup>2</sup> = 67%\*\*\* in the 400-s samples), a pattern seen otherwise only in expt 2. Since in expt 2 a high



**Fig. 1.** Correlations between the arrival rate of tsetse flies (*G. pallidipes*) at an odour-baited target and the concurrent mean wind speed in different situations. A (expt 1): 10-min samples at a 1-m<sup>2</sup> black screen in thick 'mopani' scrub; for winds up to 0.6 m s<sup>-1</sup> regression (dotted) =  $-0.55 + 124x$  ( $r^2 = +52\%^{***}$ ); for winds above 0.6 m s<sup>-1</sup> regression (dotted) =  $63 - 30x$  ( $r^2 = -11\%^{**}$ ); for the best fit curvilinear relationship (dashed,  $r^2 = 13\%^{**}$ ). B (expt 7): 10-min samples at a 1-m<sup>2</sup> blue screen in bushy grassland ( $r^2$  for the curvilinear regression =  $16\%^{***}$ ). C (expt 5): 5-min samples at a model 'warthog' in open, dry season 'mopani' (regression =  $23.7 - 13.0x$  ( $r^2 = -31\%^{***}$ )). D (expt 4): 20-min mark-release samples at a model 'warthog' in same situation as C; open circles and dotted line, 50-m releases; closed circles and broken line, 75-m releases (both logit de-transformed) overall  $r^2 = -11\%^{*}$  (data from Griffiths *et al.*, 1995). For asterisks see Table 2.

arrival rate/SD correlation coincided with a high correlation between the mean wind speed and its SD ( $r^2 = 80\%$ ; Table 1), a link with the wind's structure might be sought through that relationship. However, in expt 3 the wind speed/SD relationship was the weakest of all the experiments ( $r^2 = 30\%$ ), so no connection is apparent.

**Experiment 4: recaptures of marked flies at a 'warthog' (Zimbabwe).** As few marked flies were recaptured (<10 per 20-min observation), they are analysed in 20-min bins. They had in principle displaced themselves upwind only 50 or 75 m (the straight line minimum distances from their release points), but many will have flown much further (Griffiths *et al.*, 1995). The overall correlation was  $r^2 = -11\%$  (Table 2), but the negativity (and significance) are due to the four samples in high winds, without which there is no correlation (Fig. 1D).

**Experiment 5: unmarked fly arrivals at a 'warthog' (Zimbabwe).** The catches of 'wild' unmarked flies in expt 4 were pooled for analysis in 100-s, 5-min and 10-min bins. This set of observations revealed the strongest of all the correlations between arrival rate and wind speed (with  $r^2$  up to  $-31\%$ ) but negative in all cases (Table 2, Fig. 1C). The relationship with the standard deviation of the wind speed was equally strong, though also negative.

**Experiment 6: videoed arrivals at a black target (Zimbabwe).** This target was set along the wind line (cf. expt 1). All the

correlations of arrival rates against wind speed were negative, and significant, regardless of time-sample duration (Table 2). To allow for potential bias from returning flies being counted twice (Methods), the analysis was repeated for flies arriving in upwind flight only. These should have been mainly first-time arrivers, but their rate of arrival still correlated negatively with wind speed. No relationship with the variance of the wind speed was detectable.

**Experiment 7: arrivals at a blue target in grassland (Kenya).** Although the overall scatter of catch size against wind speed shows a positive correlation ( $r^2 = 9\%$ ; Table 2), this is essentially due to mean winds of less than 0.6 m s<sup>-1</sup>, since there were only six observations in faster wind (Fig. 1B) and none at or above 1 m s<sup>-1</sup> (i.e. well below the higher winds in the other experiments, Table 1). However, significantly more of the variance is explained ( $r^2 = 16\%^{***}$ ) by a curvilinear relationship fitted as for expt 1 (Fig. 1B).

**Experiment 8: arrivals at a blue target in woodland (Kenya).** These were the only catches carried out over whole days, rather than just during the afternoon activity peak, and the analysis of covariance revealed that over this longer time-span both temperature and time of day explained significant proportions of the catch deviance. Taking these factors into account, the

**Table 3.** Correlations between the proportion of *G.pallidipes* that arrive in apparently upwind flight at odour-baited targets and the wind speed (same experiments and details as for Table 2).

Sample duration	$r^2$ for various wind speed measures		
	Mean speed	% $>1/4$ or $>1/2$ m s <sup>-1</sup>	SD mean
Expt 1: Zimbabwe: electrified vertical target			
10 min	66	-35***	-40***
Expt 2: Kenya: 'warthog' with electric net			
10 min	48	+7(*) <sup>1</sup>	+5 <sup>NS2</sup>
Expt 5: Zimbabwe: 'warthog' with visual recording			
5 min	84	-7(*)	-8*
Expt 7: Kenya: electrified vertical target (grassland)			
10 min	115	-2 <sup>NS</sup>	

<sup>1</sup> Regressed log-log,  $r^2 = +12\%$  ( $P = 0.012$ ).

<sup>2</sup> True regression appears bimodal (cf. footnotes to Table 2): for winds of  $>1/4$  m s<sup>-1</sup> for up to 66% of the time, the regression is positive ( $r^2 = +15\%*$ ); for winds above that, the regression turns negative ( $r^2 = -17\%*$ ); but for the curvilinear regression  $r^2 = 25\%*$ .

relationship between catch and wind speed was again curvilinear ( $r^2 = 10\%$ , Table 2, footnote 4), virtually identical with expt 7 but now applying to a much greater range of wind speeds (see Table 1). Interestingly, about 25% of the *G.pallidipes* were caught when there was no measurable wind, so that they presumably found the target non-anemotactically.

*Experiment 8: arrivals of G.brevipalpis.* A similar curvilinear relationship occurred also in the contemporary, smaller catches of *G.brevipalpis* during these observations. This is particularly interesting since *G.brevipalpis* and *G.pallidipes* have inverse activity curves across the day (U-shaped for *brevipalpis*, inverted U for *pallidipes*; Harley, 1965), and so have inversely phased coincidences of their activity and the marked diurnal changes in wind speed that occur at Shimba). This thus provides independent evidence of the importance of wind speed on odour source location.

#### Flight direction inferred from electric nets

Arrival at an odour source in upwind flight was inferred from the proportion of the catch that was taken on the downwind-facing side of the electric nets at a target. These proportions were then regressed, as above, against the concurrent wind speeds. The correlations for all the experiments where such observations were possible are shown in Table 3. The results are difficult to interpret, since they include both very weak positive correlations in expts 2 and 5, and remarkably strong negative correlations in expt 1. Moreover, neither the direction nor the size of these correlations bear any consistent relationship with the correlations in Table 2. There was, however, a probable bimodal relationship with the percentage of the wind at above 0.25 m s<sup>-1</sup> in expt 2 (Table 3, footnote).

#### Flight direction recorded on video

The video records in expt 6 provide a more direct examination

of the relationship between the flies' flight directions and the contemporary wind. To allow time for a particular parcel of air to travel the few metres from the odour source to the target, the wind speed was analysed as both the five-point sliding mean centred on the time of each fly's recorded flight track, and as the mean of the 5 s preceding the track. As there were no detectable differences between flight tracks with the 5-m and 10-m odour distances from the videoed target (Methods), the tracks are pooled for analysis, providing a data base of 442 flight tracks plus the concurrent wind speeds and wind directions.

In the event, no arrangement of the data provides any evidence for a relationship between wind speed and the flight direction of the flies (Table 4). Although the circular distribution of the whole data set was highly significantly concentrated around the mean upwind direction ( $P < 0.001$ ; Brady & Griffiths, 1993), breaking this down into different wind speed ranges indicates no improvement in the relationship with increasing wind speed. The upwind bias is statistically indistinguishable as to either direction or upwind concentration in winds of 0.1–0.4 m s<sup>-1</sup> which should be meandering, and winds of 1.0–2.5 m s<sup>-1</sup> which should be straight (Raleigh's  $Z = 3.78$  ( $P \sim 3\%$ ) and 4.17 ( $P \sim 2.5\%$ ), respectively).

There was also no correlation between wind speed and the angles at which the individual flies flew to the wind (Table 4, bottom half), nor any difference between the mean of this angle in slow winds and fast winds. Furthermore, this lack of relationship between wind speed and flight direction applied whether the analysis looked at flies as they arrived in the field of view or as they flew out of it, whether wind speed was taken as the five-point sliding mean or as the 5-s preceding mean, and whether analysis was restricted to upwind arriving flies or to crosswind arriving flies that turned at the target (the most strongly upwind-biased responders (see Brady & Griffiths, 1993).

#### Ten-second cross-correlation data

The raw data in expts 3 and 5 were taken in 10-s time bins. This

**Table 4.** Lack of relationship between wind speed and flight directions of *G.pallidipes* revealed by video analysis of flies leaving a 1-m<sup>2</sup> vertical black target (=expt 6); no within row cells differ significantly.

	Wind speed range (m s <sup>-1</sup> )				
	0.1–0.4	0.5–0.6	0.7–0.9	1.0–1.2	1.3–2.5
No. of flight tracks ( <i>n</i> )	77	102	117	73	72
% Flying ±45° of due upwind	36	36	31	36	35
% Flying ±90° of due upwind	64	64	53	58	58
Correlation ( <i>r</i> <sup>2</sup> ) for flight angle vs wind angle <sup>1</sup>	0.1%		–	0.2%	

<sup>1</sup> Correlations for regression of flight direction on wind direction for wind bins of 0.1–0.6 and 1.0–2.5 m s<sup>-1</sup> (*n* = 70 and 65) computed for flies arriving crosswind (the most strongly upwind-responding flies; see Brady & Griffiths, 1993).

is a much finer time-scale than that previously assumed to be involved in flight up odour plumes (e.g. Vale, 1977; Bursell, 1988) but is relevant to that involved in 'fast' upwind flight to a source (Griffiths *et al.*, 1995). It thus in principle permits the use of lagged cross-correlations to look for evidence of a relationship between the arrival of flies and gusts of wind that passed the odour source, travelled away from it, and then influenced the flies' upwind orientation tens of metres away downwind. There were twenty-eight sequences lasting 250–350 s suitable for analysis.

Although this yielded more positive correlation peaks than negative (31 +ve versus 20 –ve for *r*<sup>2</sup> ≥ 10%), most of these were not significant statistically. There were fourteen significant positive peaks (*P* ≤ 0.05 or better) against only six significant negative peaks, but 14:6 is not significantly different from a random 50:50 ratio ( $\chi^2$ ), so conclusions are not obvious. At best one might suggest that these cross-correlations indicate that faster winds several metres away from an odour source provide better guidance towards the source than does the wind at the source.

## Discussion

### Sources of variance

Few of the regressions of arrival rate against wind speed explain more than a small proportion of the variance. Clearly, there are both environmental and behavioural sources of this unexplained variability. Behavioural complications are outlined in the Introduction, and are not readily mitigated. Potentially significant environmental factors – apart from the wind – include vegetation, temperature, and time of day. These were either allowed for in the analysis, or seem unlikely to be important, for the following reasons.

**Vegetation.** The experimental sites in expts 4–7 were either almost leafless or in short grassland, whereas the bush in expts 1, 2, 3 and 8 was much thicker. There were, however, no consistent differences in the wind that are obviously associable with this nor with any other different vegetational topographies (Table 1).

**Temperature.** All the observations (except expt 8) were performed during the peak activity hours of *G.pallidipes* between about 15.00 and 18.00 hours, during which the temperature changed by less than 2°C on any one day (and by <–5°C between days). A statistical association between arrival rates and

temperature was found in expts 4, 7 and 8, which suggested rising recapture rates up to –32°C but falling rates above that (i.e. as in the inverted 'U' reported for field activity; Brady & Crump, 1978), but this was allowed for in the analysis of covariance.

**Time of day.** Experiments 1, 2, 7 and 8 lasted long enough to be potentially influenced by diel changes in the activity level of *G.pallidipes*, but the analysis of covariance in expts 1, 7 and 8 allowed for time of day effects, and in expt 2 the correlations were unaffected by the time of catch. In the other experiments observations lasted less than an hour, and so cannot have been influenced by activity changes over time.

### Arrival in upwind flight

The relationship between the tendency to arrive at a source in upwind flight and the wind speed is ambiguous (Table 3). Moreover, although the total catch often correlated highly significantly with the wind speed (Table 2), in no case was there a significant correlation between the proportion caught in apparent upwind flight and the total catch. There was also no detectable relationship between the direction of flights and the concurrent wind speed in the video observations (Table 4).

It was only in expt 1 that any strong correlations occurred, but these were negative, and it may be that they were due to eddies on the lee-side of the target. Lee-side turbulence will inevitably have increased as the wind increased, because the target consisted of 2 m<sup>2</sup> of cloth and netting set across the wind, and that may well have affected the flies' final approach to the target. Such eddies would, on the other hand, have been far weaker around a model warthog upwind of an electric net, as used in expts 2 and 5.

### Why so few upwind flights?

If tsetse flies do find odour sources in upwind flight, as all the evidence indicates (see Colvin & Gibson, 1992), why did we find upwind arrival so hard to detect? Probably because upwind arrivals are obscured in the 'noise' of tsetse flies swirling around visual targets (see Gibson *et al.*, 1991), since all previous observations show upwind anemotaxis against a background of many tsetse flies flying at random with respect to the wind.

Video studies in synthetic host odour, for example, typically reveal only 40–50% of flights within  $\pm 60^\circ$  of upwind, when random expectation would be 33% anyway (Brady & Griffiths, 1993; and Table 4 above), or 70–80% flying upwind when 55% of no-odour controls are doing so (Gibson *et al.*, 1991). Likewise, experiments with rings of electrocuting nets, whether baited with real or synthetic ox odour, typically catch only about 60% or 70% on their downwind-facing sides, when random expectation would be 50% (Vale & Hargrove, 1979; Torr, 1989; Torr & Mangwiro, 1995). Also, the best upwind take-off orientation is ~55% when random expectation is 25% (Bursell, 1987).

Upwind fliers in host odour are therefore normally less than twice as common as random expectation. Moreover, whenever the wind falls below about  $0.5 \text{ m s}^{-1}$ , which it frequently does in tsetse bush (Brady *et al.*, 1989), the air will be moving an order of magnitude slower than the flies are (Brady, 1991), and may then provide such weak optomotor cues from wind drift (see David, 1986) that the flies cannot steer upwind. At that point simpler kinetic responses to odour presumably supervene (Warnes, 1990; Gibson *et al.*, 1991; Paynter & Brady, 1993).

#### *Flight duration and the role of anemotaxis*

It seems from recent work (Griffiths *et al.*, 1995) that tsetse flies locate distant odour sources by two methods: a one-step, 'aim-then-shoot' sequence, which is fast if the initial aim was in the right direction (<30 s for 30–75 m); and an anemotactically-guided 'search', which should be a more reliable way to find a source (Williams, 1994) but may take much longer. The 'aim-then-shoot' strategy is presumably influenced by wind direction mainly at take-off (Bursell, 1987; Torr, 1988), and Griffiths *et al.* found the probability of such one-step flights occurring to be weakly inversely related to wind speed. The 'search' strategy, on the other hand, can take so long that the direction of odour-bearing wind might influence the fly's flight for several minutes.

It was therefore of interest to know whether there were different relationships between arrival rates and wind speed sampled on different time scales. In a limited sense it seems that there are. In expts 3 and 5, as the length of the time-sample is extended, even though the numbers of samples then inevitably decrease, the correlations with mean wind speed improve – dramatically so for the standard deviation (Table 2).

This is not an artefact of sample length, since the samples are all longer than the minimum 'reliable' wind sample of ~2 min (Griffiths & Brady, 1995). It may therefore indicate that the longer flights do, indeed, correlate better with longer wind samples. On the other hand, it is highly unlikely to apply to the fast flights, because then the individual fly's orientation will often have been completed within a wind episode not reflected by the mean (although there was little direct evidence for this in the cross-correlation study).

#### *Relationships with the wind speed*

The correlations between arrival rate and wind speed were negative in expts 4, 5 and 6, sometimes strongly so (Table 2). This had

not been expected from the plume-straightness/wind speed relationship. However, the scatter plots for these data sets are triangular, in the sense that both low and high arrival rates occurred in the low wind speed range, but only low arrival rates occurred in high winds (Figs 1C and 1D). Thus, it was mainly (or exclusively) the proportion of the wind that was relatively fast that accounted for the negative correlations.

Thus, in expt 4, the overall regression is close to zero without the four observations which took place in mean winds above  $1.25 \text{ m s}^{-1}$ ; in expt 5 the negative regression is significant only if the catches in wind above  $0.6 \text{ m s}^{-1}$  are included; and in expt 6 it is significant only if the catches in winds above  $1.0 \text{ m s}^{-1}$  are. This is consistent with Warnes's (1992) wind-tunnel observations, in which there was a marked reduction in spontaneous take-off by *G. pallidipes* in winds above about  $0.5 \text{ m s}^{-1}$ .

It may also be that the lack of correlation between arrival rate and wind speed in low winds arises because of the variability in the wind's speed over time. This may distribute above threshold odour over a wider area, by a combination of meandering slow phases spreading a more concentrated plume laterally, followed by faster phases translocating these broad swathes further away downwind. That might stimulate more tsetse to fly upwind, but would only be of significant use to the flies that hit the odour patch near the source, and therefore in low wind-speed episodes. Their location of the source thereafter could then be mainly chemokinetic, but would paradoxically suggest better odour location in slower winds. The high correlations of arrival rate with the variance in the wind speed in expts 2 and 3 (though not expt 5, where it is negative) would accord with this.

#### *A bimodal relationship with wind speed?*

Several of the data sets show a significant *bimodal* relationship between catch and wind speed, with arrival rates increasing as the wind increased in weak winds, but then decreasing in still higher winds. In expt 1, for example, although there is a strong positive correlation of arrival rate with winds up to  $\sim 0.6 \text{ m s}^{-1}$ , above that the correlation turns significantly negative (see footnote, Table 2). Similarly in expt 3, although arrivals correlate positively with the proportion of wind that was faster than  $0.25 \text{ m s}^{-1}$  ( $r^2 = +14\%$ ), the correlation is negative with the proportion that was over  $0.8 \text{ m s}^{-1}$  ( $r^2 = -27\%$ ). And in expt 2, the tendency to arrive in upwind flight correlates positively with the proportion of the wind faster than  $0.25 \text{ m s}^{-1}$  for up to two-thirds of the time ( $r^2 = +15\%$ ), but negatively in winds above that ( $r^2 = -17\%$ ; Table 3, footnote). Likewise, in expt 7, the positive correlation applies, in effect, only to winds of up to  $\sim 0.6 \text{ m s}^{-1}$ , since all six catches that occurred in faster winds were low.

In fact, the curvilinear fits for multiple regressions in expts 1, 2, 7 and 8 (Figs 1A and 1B) explain more of the variance than any transformed linear analysis. In these cases, therefore, there was an improvement in the flies' odour-locating performance as the wind increased to about  $0.5 \text{ m s}^{-1}$ , but a fall-off in performance as the wind increased beyond about  $1.0 \text{ m s}^{-1}$ .



### Turbulence and anemotaxis

Yet another complication to the interpretation of the data is the relationship with wind turbulence, which will affect the immediate wind direction the flies detect. Tsetse flies (and other wind-orienting insects) encounter turbulence in two different situations: at rest, and in flight. At rest (which tsetse are for 99% of the time; Brady, 1972, 1988), they will be at a point fixed in space, and will mainly be exposed to turbulence on a scale much finer than that which activates an anemometer. We know little about such fine-scale turbulence, but observations with ultra-light wind vanes <5 cm long suggest that, at the centimetre scale, increasing wind speed provides increasingly more unreliable directional information at a fly's twig or branch resting site (Brady *et al.*, 1989; and unpubl.).

In flight, on the other hand, the flies are borne in and on the wind (as is the odour) and, by flying at around 5 m s<sup>-1</sup> in winds that are almost always less than 2 m s<sup>-1</sup> and are often much less than 0.5 m s<sup>-1</sup>, they will pass into, through and out of odour plumes rapidly, regardless of the wind's direction. Moreover, they will fly through turbulence of the kind 'seen' by an anemometer (which is scaled at ~15 cm diam.) in fractions of a second, whereas their orientational turns have diameters of around 1–2 m (Gibson & Brady, 1985, 1988).

In marked contrast to the situation experienced by moths, therefore (see e.g. Murlis *et al.*, 1992), odour plumes may often be functionally stationary for anemotactically orienting tsetse. So, although they undoubtedly respond anemotactically in host odour, their biased random walk towards a source (Brady *et al.*, 1990; Williams, 1994), may be influenced more by kinetic responses than has previously been supposed (except by Warnes, 1990).

There is now gathering evidence that moths are much 'concerned' with the fine structure of the odour within a pheromone plume. Whether they zigzag across wind or fly almost straight up is a complex function related to turbulence and distance from the source (e.g. Liu & Haynes, 1993). The control system operates in terms of the rate at which above threshold wisps of odour are detected by the moths' antennae (Mafra-Neto & Cardé, 1994; Vickers & Baker, 1994). It is entirely possible that tsetse, too, are sensitive to the fine structure of their hosts' odour plumes – though presumably on a different time-scale – and that their success at finding hosts is as much to do with that as the way the whole plume moves through the bush.

### Odour plume structure

Current models of odour dispersion in plumes indicate greater dilution of the odour with increasing wind speed due to the greater turbulence in higher winds. Hence, as the wind increases there is a smaller 'active space' of the plume (see Introduction and Elkinton & Cardé, 1984; Murlis *et al.*, 1992). It may thus be that what constrains flies in finding an odour source anemotactically is the interaction of improving plume straightness as the wind speeds up, opposed by the reducing area of the effective plume as the same total amount of odour is smeared out over a greater distance downwind.

Our results in fact suggest that tsetse flies have difficulty in locating odour sources both in very low winds *and* in fast winds. The former is to be expected for anemotactically navigating flies because of the wind's highly non-linear movement at very low speeds: the flies' source-finding performance in such winds presumably improves as the wind speeds up and straightens out. The latter might be predicted from the reduction in functional plume width with increased wind speed, which will reduce the recruitment of flies from downwind (with reduced take-off frequency in high winds (Warnes, 1992) presumably adding to the effect). Nakamura (1976) seems to be the only other person to have directly studied this problem in the field, and he was puzzled by a similar (though doubtfully significant) dual relationship with wind speed in his moths' mean response distance to a pheromone source: it appeared to increase in winds up to ~1 m s<sup>-1</sup> but then to decrease in winds above that.

We conclude that our initial premise was half correct: odour source location by tsetse does, indeed, improve somewhat with increasing wind speed within the range that straightens out odour plumes (i.e. in winds up to around 0.75 m s<sup>-1</sup>; see Griffiths & Brady, 1995, Fig. 4). On the other hand, as the wind becomes still faster, even though it then blows virtually straight overall, its increased turbulence effectively dismantles the odour plume, and so makes the location of hosts increasingly harder for the flies.

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