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Diel activity patterns and host preferences of *Glossina fuscipes fuscipes* (Diptera: Glossinidae) along the shores of Lake Victoria, Kenya

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Abstract

Diurnal activity patterns and host preference of *Glossina fuscipes fuscipes* Newstead were studied in forest and linear habitats along Lake Victoria shore, Kenya. The objective was to identify the preferred hosts of *G. f. fuscipes*, the emanations of which may be attractive to this species. Hourly catches of flies in biconical traps were related to changes in the weather and the prevalence of hosts in the vicinity of traps. Flies were mainly active between 0800 and 1600 h, with males peaking around 1100 h and females around 1300 h. Activity of flies correlated directly with light intensity and temperature, but indirectly with relative humidity. Humans, livestock and the monitor lizard, *Varanus niloticus*, were the predominant hosts, although a significant positive correlation with fly catches could only be established with the prevalence of lizards. Blood meal identification by microscopic and serological methods showed that 73–98% of *G. f. fuscipes* fed on monitor lizards irrespective of host prevalence, season or location. The significance and possible epidemiological importance of the relationship between *G. f. fuscipes* and monitor lizards are discussed.

Introduction

Early studies on blood meals of tsetse flies, *Glossina* spp., were concerned with the identification of their preferred hosts. Elimination or eviction of such hosts was expected to starve tsetse to death, thus achieving control of trypanosomiases. However, host preference studies have acquired new dimensions, since the discovery of the attractiveness of bovine breath and urine to some tsetse species (Vale, 1974a; Owaga, 1984). By dispensing economical but potent doses of olfactory baits derived from preferred hosts near insecticide-treated targets (Vale *et al.*, 1988; Willemse, 1991) or untreated traps (Dransfield *et al.*, 1990), control of *G. pallidipes* Austen, *G. m. morsitans* Westwood and *G. m. centralis* Machado (Diptera: Glossinidae) was achieved.

To date, no effective olfactory bait, apart from CO_2 (Frezil & Carnvale, 1976), has been discovered for any of the species of the riverine *palpalis* (Robineau-Desvoidy) group of tsetse. Flies of this group are opportunistic feeders, obtaining their blood meals from any available source, presumably using visual cues for host location (Weitz, 1970; Laveissiere *et al.*, 1990; Moloo, 1993). Where *palpalis* tsetse feed mainly on certain hosts (e.g. reptiles), this has been attributed to the high prevalence of such hosts and/or their complacency to attack by flies. This issue needs to be re-examined and substantiated in order to develop effective control strategies for this group of flies.

We investigated the host preferences of *G. f. fuscipes* Newstead along the shores of Lake Victoria, Kenya using hourly biconical trap catches of engorged flies from three distinct habitats. These hourly catches were related to diurnal changes in host prevalence together with corresponding changes in weather. A preliminary experiment on host preference was also carried out by presenting flies with stationary hosts including monitor lizards, a human, a calf and a goat enclosed in an incomplete ring of electric nets (Vale, 1977). The main objective of these studies was to identify the preferred host(s) of *G. f. fuscipes*, the emanations of which could be attractive to this species and, possibly, other members of the *palpalis* tsetse group.

Materials and methods

Study area

The study was conducted between May 1992 and

December 1993 along a 45-km strip of the Lake Victoria shore, Mbita Division, Homa Bay District, Western Kenya (fig. 1). The topography, demographic characteristics, climate and vegetation of the area have been described by Mwangelwa *et al.* (1990). The climate is generally equable with no clear seasons. The vegetational cover has been affected by human activity with many clearings for subsistence farming. The lacustrine bush which shelters tsetse has, in effect, been reduced to forest patches and thicket clumps. Humans and domestic animals (cattle, goat, sheep) as well as monitor lizards, *Varanus niloticus niloticus* Laurenti, are probably the main available hosts for *G. f. fuscipes*. Most of the wildlife, apart from hippopotamus, *Hippopotamus amphibius*, have either been hunted out or driven away by destruction of habitat.

Three representative tsetse habitats were selected for the present study (fig. 1):

H1. A *Lantana* hedge habitat at the ICIPE Guest House, Mbita Point Field Station (MPFS), which harbours a medium tsetse density of up to 100/trap/day. Monitor lizards and humans were the available tsetse hosts at this location.

H2. A habitat of linear forest patches at Kissiwi which has a fairly high tsetse density of up to 200/trap/day. The tsetse hosts at this location were humans, cattle, goats, sheep, donkeys, dogs, monitor lizards and duikers.

H3. A small (*c.* 120 ha) dense forest at Ungoye Research Site, ICIPE. The forest is heavily-infested with tsetse (up to 500/trap/day). Here, potential hosts were cattle, sheep, goats, duikers, hippopotamus (during breeding season), monitor lizards, green monkeys and dogs.

Methods

In each habitat, two permanent trapping sites at least 200 m apart were selected. Except at H1, one trap site was chosen near a known watering point for man and livestock and the other site located where human activity was relatively low. At each trapping site a single unbaited biconical trap (Challier *et al.*, 1977) was set for four cloudless days of each month from May 1992 to December 1993. Trap catches were collected at hourly intervals from 0600 to 1800 h. Ambient temperature (°C), percent relative humidity (r.h.) and light intensity (lux) were simultaneously recorded at both trapping sites at 30 min intervals. Temperature was measured by minimum and maximum thermometers in shade 1 m above ground level, r.h. by wet-bulb whirling hygrometers and light intensity by light meters, (Li-COR®, MODEL Li-189, USA). Due to a delay in the arrival of equipment, data on light intensity and r.h. were obtained only during the last six and twelve months of the study, respectively.

The numbers of humans, livestock and monitor lizards

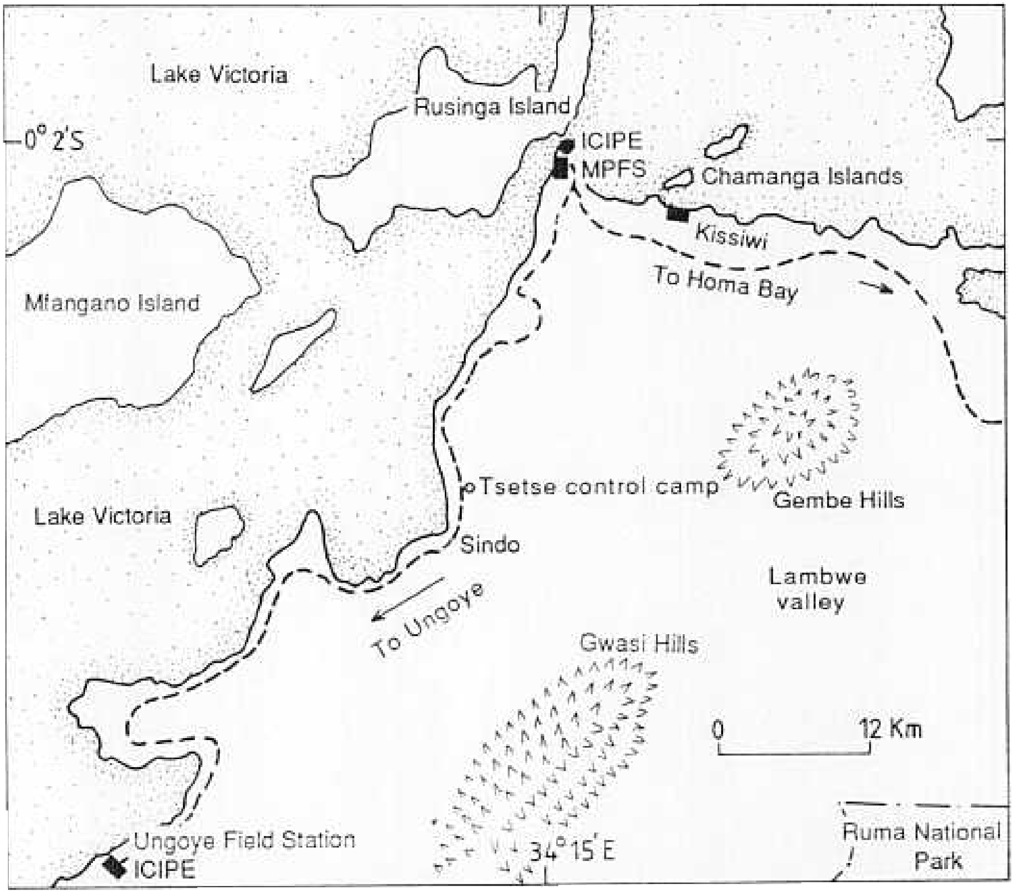

Fig. 1. Map of the study area showing the three trapping sites.

sighted within 10–30 metres of a trap were recorded every 10 min by an observer who quietly approached the vicinity from about 50 m away. Separate records were kept for species of animals as well as men and women. Data on lizards were available throughout the study, but those on humans and livestock covered only the period from May to December 1993.

In each habitat, hourly catches of flies were killed, sexed and counted. Due to intervention by ground spraying of cypermethrin between October and December 1992, data on tsetse activity, host prevalence and weather factors were not possible at H1 and H3 after the first three months and six months, respectively. The studies continued uninterrupted at H2 because the samples were taken just before the spray in November and one month later in late December 1992 when monitoring showed that an adequate number of flies (30–50 as against 70–120/trap/day in the pre-spray period) was present. Except at H1, the spraying was generally ineffective and H3 had to be resprayed in September 1993 (unpublished data). However, despite interruptions at H1 and H3, collections of blood meals were available from monthly sampling for assessment of the effects of the spraying operation.

Although few fully engorged tsetse are found in 24-h biconical trap catches, the collection of flies at hourly intervals and subsequent dissections for undigested residual blood helped to secure adequate samples of fed flies for comparative purposes. To determine host preference, smears were made of the gut contents of flies which, by external appearance or after dissection, were judged to contain undigested blood. The source of the blood meal was later identified by enzyme linked immunosorbent assay (ELISA) at the Robert von Ostertag Institute, Berlin, Germany. Moreover, blood meals from lizards or other reptiles were locally identified by microscopic examination (×400) of wet smears of the gut contents. Lizards (and other reptiles) have large, elongate nucleated red blood cells (RBC) as distinct from the relatively smaller, round non-nucleated mammalian RBC. Microscopic examination has the additional advantage of distinguishing blood meals containing scanty amounts of undigested blood. Reptilian blood meals identified by microscopy were all attributed to monitor lizards because ELISA did not reveal any other reptilian host.

Since preliminary blood meal analysis showed that the monitor lizard was the preferred host of tsetse, confirmatory experiments for the preference of lizards were conducted using an incomplete ring of five 1-m^2 electric nets placed around tethered baits (Vale, 1974b, 1977). The ring of nets (diameter 4 m) was placed separately around two monitor lizards (10 kg), a black male calf (100 kg), a black male goat (20 kg) and a human (male, 60 kg) at H3. Each bait was tested for 7 consecutive days to avoid possible effects of host residues on fly catches. Each day consisted of a morning run (900–1200 h) and an afternoon run (1400–1700 h). Although such an experimental design might have influenced the number of tsetse approaching each bait, the main objective of the experiment should not have been compromised. The objective was to estimate the relative feeding success of *G. f. fuscipes* on the different baits from relative proportions of fed and unfed flies caught on the inside face of the nets. Flies electrocuted on either face of the nets were retained as they fell on corrugated iron trays smeared with a sticky deposit and placed beneath the nets. Fed flies caught inside the ring were assumed to have fed on the host.

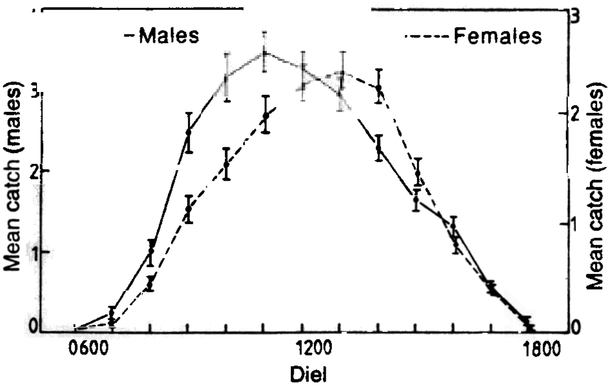

Fig 2. Diel activity of male and female *Glossina* *ipes fuscipe* bars represent the s.e.

Statistical analysis

Unless otherwise stated, all analyses were carried out on the comprehensive data available for H2 (Kissiwi) only. Due to the close similarity in the daily diel rhythms, all data for both trap locations at H2 were combined. Data on men and women were grouped as human, while those on goat, sheep and cattle were grouped as livestock.

The activity profiles of male and female tsetse were obtained by plotting the mean hourly catches (±S.E.) of either sex against time. Similar profiles were plotted for host prevalence and the meteorological recordings. The peak catches of flies were identified from these plots and superimposed on those of host and weather.

Correlation analyses were used to relate fly catches to both weather factors and host prevalence lagged for 0, 1 and 2 h. Path coefficient analysis (Wright, 1934; Nie *et al.*, 1975) was used to separate the direct effects of host prevalence from their indirect effects, through the meteorological variables, on fly catch. The assumption was that since the activities of hosts are influenced by the weather, the hosts will both directly and indirectly (by acting in combination with the meteorological variables) influence fly catch. Hence, the need for partitioning the total effect of a host on fly catch as measured by the correlation coefficient. Path analysis permits this separation. The direct effect of a host is a measure of its influence on fly catch given that all the climatic factors are held constant.

Prior to the analyses above, fly catches, number of hosts and light intensity data were transformed to the logarithmic scale ($\log_{10}$) while percentage relative humidity data were transformed to the arcsin scale.

Results

Diel activity

The activity rhythms of both male and female *G. f. fuscipes* (fig. 2) showed unimodal patterns, but with clear differences. Catches of either sex were extremely low up to 0800 h. Thereafter, male catches increased sharply to reach a peak at about 1100 h after which they declined gradually until sunset (fig. 2a). From 0800 h female catches increased relatively slowly, culminating in a peak at about 1300 h, followed by a steep decline until sunset (fig. 2b).

The corresponding diurnal patterns of the hosts and the abiotic factors are presented in figs. 3 and 4, respectively. The correlations between these variables and the diel changes in fly catches are summarized in table 1. Male and female catches were positively correlated with lizard prevalence; the correlations being higher with females than males and highest for either sex or both combined without lags. In contrast to the lizards (fig. 3a), the prevalence of humans (fig. 3b) or livestock (fig. 3c) was negatively correlated with fly catches (table 1).

Considering the effects of the abiotic factors (fig. 4a,b,c), hourly fly catches were positively correlated with light intensity and temperature, but negatively with relative humidity (table 1). The correlations with each of these variables decreased with hourly lags, indicating that the effects of these weather factors on fly catches were almost immediate.

The results of the path coefficients analysis (table 2) confirmed that the presence of lizards had a significant positive direct effect on fly catches while that of humans or livestock had significant negative effects. It further showed that livestock had a more pronounced negative effect than humans though it was masked by the indirect positive effect of light intensity. All hosts, however, had significant indirect effects on fly catches by acting in combination with light intensity. The indirect effects of the hosts in combination with relative humidity and temperature were negligible (table 2).

Host preference

The identity of 857 blood meals, obtained from the three habitats over 20 successive months, is presented in table 3. Although 4–5 times more flies with undigested blood were discovered by microscopy than by ELISA, similar results were, however, obtained by both methods as regards the proportion of feeds from monitor lizards. Both methods show that there was no relationship between the relative abundance of host species and the frequency with which they were fed on by *G. f. fuscipes*. Although the apparent prevalence of lizards near traps was only about 2.5% of all other hosts (table 4), 94.0–98.4% of the blood meals in the linear habitats (H1 and H2) were obtained from these reptiles. In the dense forest (H3) the trend in feeding pattern was also similar to H1 and H2: 78.0–83.2% of males and females fed on monitor lizards; the remaining meals were drawn from cattle, man, dogs, wild ruminants and suids. Thus, along Lake Victoria shores, monitor lizards seem to be the main food source for *G. f. fuscipes*.

Feeding success on baits

The results of this preliminary experiment showed that more flies approached and fed successfully on monitor lizard than on cattle, goat or man (table 5). The number of feeds on man and goat was too small to permit Chi^2 analyses, but for the lizard/calf comparison significantly more tsetse had fed on monitor lizard than on the calf (Chi^2=4.30, df=1, $P<0.04$). Furthermore, if we consider the number of flies per replicate (table 5), it can be seen that significantly fewer flies approached and ventured inside the ring when man was the bait than when the ring was empty (t=5.00, df=16, $P<0.02$).

Discussion

The diurnal distribution of catches of *G. f. fuscipes* recorded in this study was similar to that reported by Harley (1965) for the same species from stationary bait oxen at Lugala, a climatically similar area situated at the north-eastern shore of Lake Victoria, Uganda. Both populations were most active between dawn and late afternoon with a single peak for either sex, and males peaking before females. Such activity patterns were, however, slightly different from those of Mwangelwa *et al.* (1990) who noted that on the neighbouring Rusinga Island (fig. 1), female *G. f. fuscipes* peaked earlier than males and both sexes showed only one peak before noon.

Although all meteorological variables studied produced

Table 1. Correlation coefficients showing the relationships between hourly fly catches and corresponding changes in host prevalance and climate along the shore of Lake Victoria, Kenya.

Variable	Hour lag	N	Male	Female	Total
Lizard	0	988	0.197**	0.222**	0.244**
	1	912	0.173**	0.218**	0.225**
	2	836	0.057ns	0.142**	0.127**
Human	0	988	−0.154**	0.142**	−0.168**
	1	912	−0.166**	0.157**	−0.188**
	2	836	−0.187**	0.164**	−0.210**
Livestock	0	975	−0.035ns	0.026ns	−0.001ns
	1	900	−0.067**	−0.023ns	−0.067*
	2	825	−0.154**	−0.125**	−0.152**
Light intensity	0	728	0.526**	0.540**	0.627**
	1	672	0.329**	0.398**	0.422**
	2	616	0.073ns	0.133**	0.109**
Relative humidity	0	1195	−0.275**	−0.252**	−0.310**
	1	1104	−0.153**	−0.164**	−0.180**
	2	1012	−0.019ns	−0.50ns	−0.028ns
Temperature	0	1703	0.428**	0.479**	0.521**
	1	1573	0.189**	0.268**	0.250**
	2	1441	−0.061*	0.030ns	0.045ns

N, number of observations; ns, not significant; *, **, significant at $P<0.05$ and 0.01, respectively

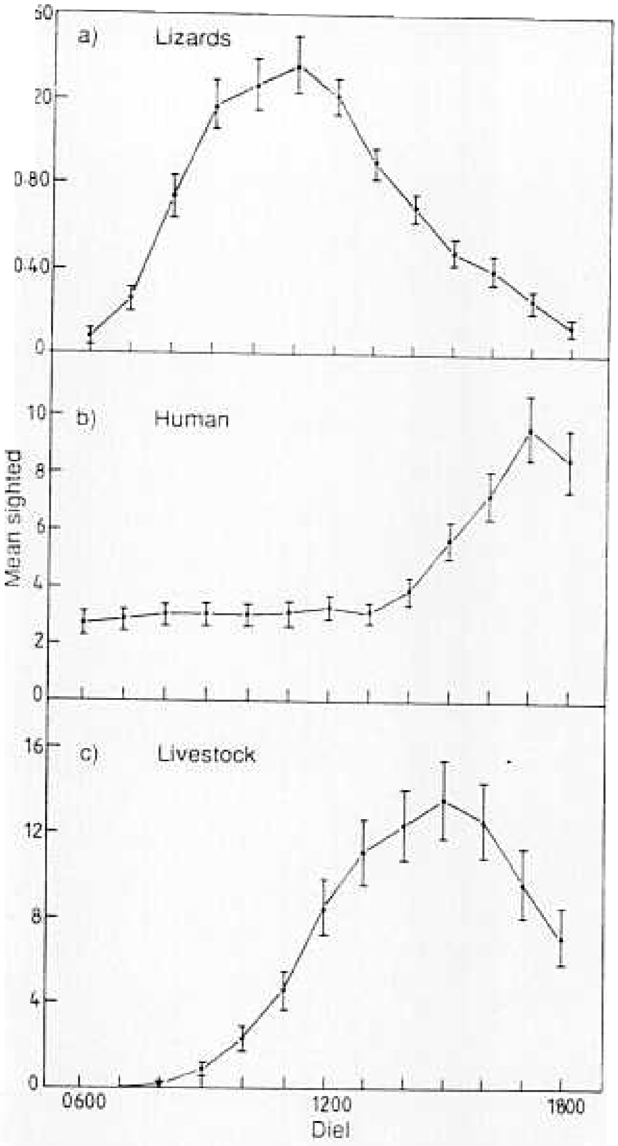

Fig. 3. Diel prevalence of hosts (a) lizard (b) human (c) livestock. Means were calculated from records taken at 10-min intervals in each hour; bars represent the s.e.

statistically significant relationships with the rhythms of *G. f. fuscipes*, catches of both sexes correlated best with light intensity. Comparable results were reported for the same species by Oloo (1983) and Mwangelwa *et al.* (1990) at similar localities on the Lake Victoria shore.

Of all groups of hosts seen near traps, only the presence of lizards enhanced fly catches in traps. On the other hand, maximum numbers of livestock and humans were observed in the afternoon when the tsetse trap catches were declining simultaneously with light intensity and temperature. This might partly account for the observed negative correlations of humans and livestock with fly catches since peak prevalence of these coincided with a period of apparent low activity of the fly. Alternatively, the presence of humans and livestock in large numbers near the traps might have scared away the preferred hosts (lizards) with the flies following. However, the results of the path coefficient analyses (table 2), which are standardized partial regression coefficients (Nie *et al.*, 1975), emphasized the enhancement of fly catches by the presence of monitor lizards as opposed to the adverse effects of humans and livestock. The analysis further shows that the adverse effects of these latter hosts on fly catches were present throughout, but were mitigated by weather factors, particularly higher light intensity at the earlier parts of the day (table 2). These findings have important implications.

Firstly, as with *G. pallidipes* and *G. m. morsitans* (Vale, 1974a), the presence of the observer who monitored host prevalence near traps might have influenced trap catches by interfering with the normal responses of *G. f. fuscipes* to

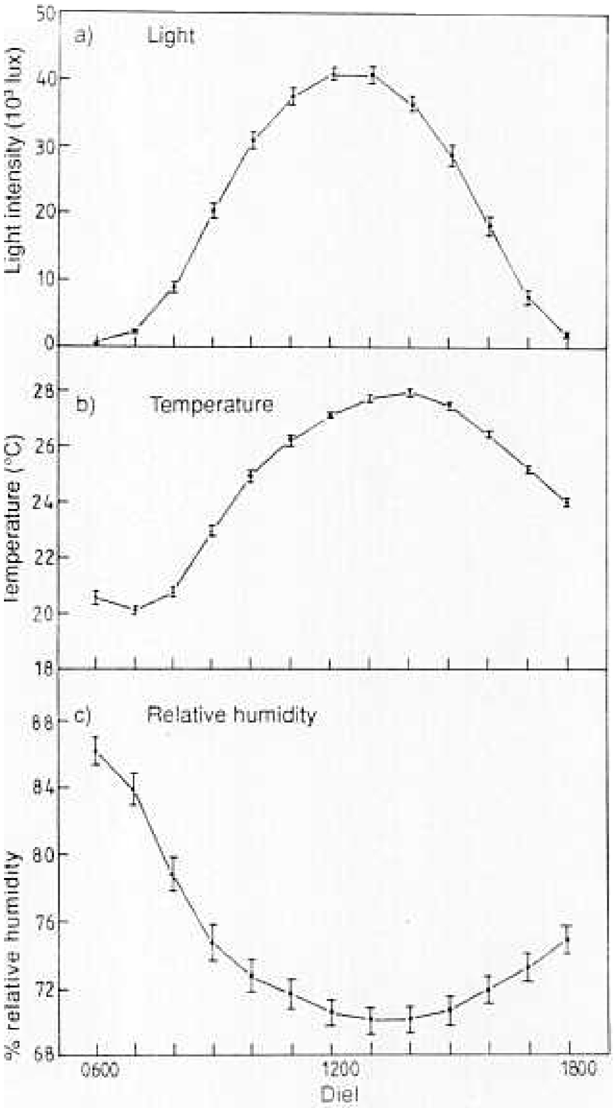

Fig. 4. Diel records of abiotic variables (a) light intensity (lux) (b) temperature (°C) (c) % relative humidity. Means were calculated from recordings taken at 30-min intervals per hour; for temperature each record was obtained by computing (minimum+maximum)/2; bars represent the s.e.

Table 2. Path-coefficient analyses of direct correlations between hourly catches of *Glossina fuscipes fuscipes* and host prevalance and influence of weather on these correlations.

Host	Influence via	Male	Female	Total
	Direct	0.100**	0.133**	0.134**
	Light intensity	0.085*	0.079*	0.099**
	Relative humidity	−0.011ns	−0.030ns	−0.022ns
	Temperature	0.023ns	0.040ns	0.034ns
Livestock	Direct	−0.669**	−0.554**	−0.716**
	Light intensity	0.606**	0.534**	0.677**
	Relative humidity	0.019ns	−0.018ns	0.005ns
	Temperature	0.010ns	0.064*	0.033ns
Humans	Direct	−0.096**	−0.081*	−0.096**
	Light intensity	−0.065*	−0.062*	−0.078*
	Relative humidity	−0.002ns	−0.015ns	−0.009ns
	Temperature	−0.010ns	0.016ns	0.014ns

ns, not significant significant at P=0.05 and 0.01, respectively.

Table 3. Proportions (%) of *Glossina fuscipes fuscipes* fed on monitor lizards in the three habitats along the shore of Lake ictoria, Kenya as determined by ELISA in Germany or locally by microscopy, April 1992 to December 1993.

Method	Habitat	Total	No. fed (%)	No. identified	% Fed on monitor lizards		
					Male	Female	Total
ELISA	H1	1612	104 (6.5)	94	97.8	97.9	97.9
	H2	6397	271 (4.2)	246	98.0	98.4	98.4
	H3	2240	177 (6.7)	149	85.2	76.5	83.2
	Total	10,249	552 (5.4)	489	93.3	94.9	93.7
Microscopy	H1	520	160 (30.8)	160	91.9	97.3	94.4
		595	137 (23.2)	137	94.9	95.9	95.6
		289	71 (24.6)	71	73.1	94.7	78.9
		1404	368 (26.2)	368	87.0	96.3	91.8

H1, *Lantana* hedge, MPFS, ICIPE: H2, linear forest, Kissiwi; H3, dense forest, Ungoye (fig. 1

traps and probably also by the disturbance of lizards in the vicinity. Secondly, since cattle seemed to be a non-favoured host, control by 'pour-on' insecticide using these animals may not be effective against *G. f. fuscipes* or other riverine species extant with savanna tsetse. In Burkina Faso, Bauer *et al.* (1995) reported that deltamethrin 'pour-on' treatment of cattle was comparatively ineffective against *G. p. gambiensis* Vanderplank where the fly fed mainly on monitor lizards, although *G. m. submorsitans* Westwood was virtually eliminated. Similarly, in Ethiopia, following control with cypermethrin 'pour-on', Leak *et al.* (1995) obtained over 80% suppression of *G. pallidipes* and *G. m. submorsitans*, but with no significant effect on the sympatric population of *G. f. fuscipes*.

There have been no previous studies relating the diel patterns of tsetse to corresponding host availability and activity. The direct relationship between fly catches and prevalence of lizards observed in this study is interesting. This relationship may simply reflect an ecological 'concordance' between flies and monitor lizards: the lizards and flies are both poikilothermic (cold-blooded) animals, probably with similar diurnal activity patterns in the environment where they co-exist. There is also the possibility of a unique kairomone produced by lizards attractive to *G. f. fuscipes* which could explain the close association between lizards and tsetse. Furthermore, contrary to the behaviour of *G. pallidipes* and *G. m. morsitans* (Vale, 1974a, 1977), the result indicates there is no relationship between the size of available apparently suitable hosts and the number of *G. f. fuscipes* that approaches them and subsequently feeds. Although livestock and humans were larger than the lizards and present with the latter in time and in space, flies fed almost exclusively on the reptiles.

Table 4. Host prevalence (mean/hour) near traps at H2 (Kissiwi) along the shore of Lake Victoria, Kenya.

Host	Observation time (hours)	Total seen	Mean (±S.E.)	%
	916	1245	1.4±0.1	2.5
	416	8793	21.1±1.0	38.3
	416	13,543	32.6±2.6	59.2

Table 5. Numbers of *Glossina fuscipes fuscipes* approaching and subsequently feeding on stationary baits enclosed separately in an incomplete ring of electric nets.

Bait	Wt (kg)	Rep. s	Tsetse caught by ring of nets			
			Total	Inside	Fed	% Fed
				99	22	22.2**
				61	5	8.2
				37	4	10.8
				9	1	11.1
				10		10.0

*Numbers in parentheses indicate the average number of flies approaching/replicate with each bait; **the proportion of flies fed on lizard significantly greater than on the calf (Chi^2=4.3, df=1, $P<0.04$); Nil, no bait used.

In terms of size, a single cow, a human being or a goat may presumably present a visual (and possibly olfactory, e.g. CO_2) stimulus for flies several times larger than that of a lizard. These hosts were, nevertheless, mostly ignored in favour of monitor lizards. The higher feeding success shown by flies on the smaller monitor lizards compared with other stationary baits several times larger (table 5) confirms the above argument and unequivocally demonstrates the preference of flies for these reptiles and/or the exceptional tolerance of their bites.

Weitz (1970) described the *palpalis* group of tsetse, including *G. f. fuscipes*, as opportunistic feeders obtaining their blood meals from any available host. This has since been corroborated for *G. f. fuscipes* by Van Vegten (1971) in south-eastern Uganda and Wijers (1974) in Mfangano Island, Kenya, and more recently by Okoth (1985) and Moloo (1993) in both countries. Such opportunistic feeding behaviour has not been supported by the present study which, in contrast, revealed a very selective feeding behaviour for this species. A restricted feeding on certain groups of vertebrate hosts regardless of their relative abundance has been observed in several species of tsetse including members of the riverine group. For example, Baldry (1964) working in Nigeria observed a very close association between *G. tachinoides* Westwood and the local domestic pigs from which 94% of the tsetse fed. The preference of Savanna tsetse for suids (warthog and bush pig) and several bovids (bushbuck and buffalo) is also well documented in the literature (Glasgow *et al.*, 1958; Weitz, 1970; Snow *et al.*, 1988; Moloo, 1993).

Various attempts have been made to relate tsetse feeding patterns to their trypanosome infection rates (Ashcroft, 1959; Jordan, 1965; Ford, 1971; Tarimo *et al.* 1984). Ashcroft (1959) suggested that the product of the incidence of infection and the proportion of tsetse feeding on a given host as an index of the relative importance of an animal as a reservoir of trypanosomiasis. Ford (1971) ranked tsetse in terms of their importance as vectors of nagana on the basis of the product of the proportions of feeds on wild and domestic Bovidae. Since lizards do not appear to harbour trypanosomes harmful to mammals (Hoare, 1970, 1972), the complete dependence of *G. f. fuscipes* on them and the fact that flies do not feed much on man and livestock are probably important factors in relation to the low incidence of nagana and the disappearance of Gambian sleeping sickness along the Kenya shore and Islands of Lake Victoria (Wijers, 1974; Wellde *et al.*, 1989, Mwangelwa *et al.*, 1990). The epidemiological implication is that should the lizard population in the area become reduced for one reason or another (e.g. hunted for their skin), *G. f. fuscipes* would be obliged to find alternative hosts and this would certainly involve man and his livestock.

Monitor lizards were probably present in abundance together with tsetse during the great 1901 sleeping sickness epidemic in Uganda that also swept the present study area. Then, flies must have fed largely on lizards with some opportunistic foraging on less-favoured wild mammalian hosts including important trypanosome reservoirs (sitatunga, *Tragelaphus spekei*; bushbuck, *T. scriptus*). As these animals have now been hunted out or driven away by bush destruction, flies have few choices other than relying on monitor lizards for food. Humans and livestock clearly visit the fly habitat, and they are always at potential risk of infection. In similarly infested areas with less human activity in Uganda, trypanosomiases transmitted by *G. f. fuscipes* are still public health and economic problems, although the fly still obtains over 60% of its blood meals from monitor lizards in these locations (Maudlin, personal communication). Understanding the role of monitor lizards in the epidemiology of the disease together with the host-location behaviour of *G. f. fuscipes* is an important step towards the control of nagana and sleeping sickness along the islands and shores of Lake Victoria.

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