Glossina fuscipes fuscipes NEWSTEAD 1910 (DIPTERA, GLOSSINIDAE): COLOUR PREFERENCES, HOST-FINDING STRATEGIES AND RESPONSIVENESS TO BAITED TRAPS.

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DECLARATION

I hereby declare that the work embodied in this thesis is a result of my own investigations during the three years research undertaken under supervision at the International Centre of Insect Physiology and Ecology (ICIPE), Nairobi, Kenya and it has not been submitted before for any degree in any other University.

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DEDICATION

To the memory of my father and my grand-mother, late Kagere Bernard and Chivunanwa Mwa Buvune.

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ABSTRACT

This study was conducted on *Glossina fuscipes fuscipes*, a riverine species of Central and Eastern Africa. It focuses on (i) colour preferences, (ii) landing and feeding behaviours on a host, the Nile monitor and (iii) on the trappability in odour- and colour-baited traps. Colour preferences were studied using electric screens in the field. Colours that were found most attractive were combined to make traps. These traps were tested as visual baits, compared to the standard biconical trap Challier-Laveissière (1977). The performance of the most successful trap type was analyzed in relation with fly sex and fly abundance. It was baited with zebu urine at changing age of storage to estimate an optimum age of urine for baiting *G. f. fuscipes* traps in field conditions. Zebu urine was also tested in conjunction with acetone. Whole body odours and urine of the monitor lizard were tested as attractants too.

Royal blue relatively attracted more flies than black colour (1.7x). The peony purple red colour stimulated landing significantly more than royal blue. The attractancy of the trap colours was a function of reflectance in the blue ($P < 0.01$) and in the infrared ($P < 0.05$) ranges of the spectrum. However, very bright colours performed weakly both for attraction and for landing, suggesting that moderate chroma in the range 450-490 nm and in the near IR (750-1100 nm) largely determine the attraction of this fly.

A biconical trap with the purple red component inside, caught 1.4 times more males and 1.63 times more females ($P = 0.03$; $n = 21$); an increase of up to 3 times at low abundance sites (catch of maximum 10 flies/trap/day) was obtained. Such a trap is advisable at low densities, in routine trapping on farms and immediately after the initial fast depletion of tsetse numbers during extermination campaigns with conventional tools. A blue/red target is also proposed instead of the usual black or blue targets.

More flies approached the biconical trap in the light region 1,600-1,700 $\mu E/m^2/s$; the response of the fly became photonegative when illumination was above 1700 $\mu E/m^2/s$. The number of males attracted was associated with the presence of bushes and that of females was very dependent on illumination rather than vegetation.

G. f. fuscipes showed a significant preference for the neck of the monitor lizard ($P < 0.05$). When the Nile monitor was present in the odour chamber of a compartmentalized experimental cage, traversed by a wind flow, 61.5 to 67.5% of the flies performed an active upwind flight towards the next compartment where further search for the host occurred. Out of 100 flies that took off from the release chamber towards the varan, approximately 50% did so by ranging upwind. In nature, flies tended to aggregate at sites where monitor lizards live ($r = 0.67$; $P = 0.05$ for females and $r = 0.54$; $P = 0.03$ for males).

When acetone and 5 to 6 week-old cow urine were used together as a bait on the standard biconical trap, the highest catch indices occurred at sites with low abundance of tsetse (average catch 0-10 flies/day), 1.7 times for males and 2.3 for females ($P < 0.05$). At low abundance (0-10 flies/day) the catch index of colour or odour-baited traps was high. A strong point of inflection appeared at the abundance level of 7 flies/day, where the treatment was just as good as the control trap. At high abundance (>20 flies/day) the catch index was very low (ca. 0.25).

ملـــــــخص

أجريت هذه الدراسة على أحد أنواع ذبابة مرض النوم *G. fuscipes fuscipes.* علـى ضفـاف بحيرة فيكتوريا بجمهورية كينيا لدراسة مدى تفضيل هذا النوع وانجذابه للالوان والمؤثرات الحسية والشمية والبصرية الصادرة عن بعض عوائل هذه الذبابة (البقر والورل النيلى) وبعض المنسوجات القطنية الملونة المستعملة فى مصائد هذه الحشرة .

إتضح أن اللون الأزرق يجذب هـذه الحشرة بدرجة أفضل من اللون الاسود بينما يزيد انجذابها للون الأحمر البنفسجي بدرجة أكبر مقارنة بـاللون الأزرق وذلـك لاسباب تتعلق بانعكاس الضوء فى منطقتى اللونين الأزرق والمنطقة تحت الحمراء فى الطيف اللونى . وظهر أن الألوان القطنية الفاتحة غير مفضلة للحشرة بصورة عامة .

وضع قطعة قماش حمراء بداخل المصائد القمعية المزدوجة المستعملة لاصطياد هذه الذبابة زاد من انجذاب الذكور بنسبة ١,٣ بينما زاد انجذاب الاناث بنسبة ١,٦ ، الجدير بالذكر انه يمكن زيادة انجذاب هذه الحشرة وبنسبة تصل الى **٣ مرات** فى المناطق التى يقل فيها كثافة تواجدها .

لذلك ننصح باستخدام هذا النوع من المصائد فى المناطق التى تقل فيها اعداد هذه الذبابة بصورة عامة أو بعد عمليات المكافحة ضدها بالوسائل الاخرى . وينصح باستعمال اللونين الأزرق والاحمر بدلاً عن اللون الاسود أو الازرق أو الازرق والاسود معاً .

كان انجذاب الذباب باعداد اكبر فى المنطقة الضوئية ١٦٠٠ – ١٧٠٠ (ميكرو اينشتين/متر مربع/ث) بينما كان التأثير عكسياً عندما زادت الكثافة الضوئية عن ١٧٠٠ (ميكرو اينشتين/متر مربع/ث) .

اتضح ان انجذاب ذكور هذه الحشرة مرتبط إيجابياً بوجود الشجيرات فى المنطقة المحيطة اما فى حالة الاناث فان الاضاءة كانت هى العامل الاهم .

اوضحت نتائج هذه الدراسة تفضيل هذه الذبابة للتغذية على الورل النيلى . عند وضع الورل النيلى فى صناديق خاصة محكمة ومعرضة لحركة الهواء فإن نسبة عالية ٥ر٦١٪ – ٥ر٦٧٪ من الذباب تحركت عكس إتجاه حركة الهواء بحثاً عن مصدر الرائحة . وضح أن هذا النوع من الذبابه وفى بيئته الطبيعية يتجمع حول مناطق معيشة الورل النيلى .

أوضحت الدراسة أن بول الابقار القديم (٥ – ٦ اسابيع) اكثر جذباً للحشرة من البول المفرز حديثاً . وعند استخدام هذا البول القديم (٥ –٦ اسابيع) مع الأسيتون كمادة جاذبة للذبابة فى المصائد القمعية المزدوجة اتضح ان اعلى معدلات الانجذاب كان فى المناطق التى يقل فيها تواجد الذباب (صفر – ١٠ ذبابه /يوم) سواء باستخدام المصائد وحدها أو مصائد مذودة بالاستون وبول الابقار . وفى كلا الحالتين كان معدل انجذاب الاناث هو الاعلى مقارنة بانجذاب ذكور هذه الحشرة .

فى حالة تواجد الذبابة باعداد كبيرة (اكثر من ٢٠ ذبابة فى اليوم) انخفض معدل الجذب بدرجة كبيرة وقد تم تمثيل العلاقة بين معدلات جذب الذبابة وكثافة تواجدها بدآله عكسيه تمثل تمثيلاً صادقاً سلوك اناث هذه الحشرة فى ٨٧٪ من الحالات .

وضع اعداد ميته من هذه الذبابة داخل الشرك نجم عنه اصطياد اعداداً اقل منها فى داخله . وقد اتضح انه فى حالة اقتراب اعداداً كبيرة من الحشرة الى المصيدة فإن الانجذاب الى داخلها يقل عما اذا اقتربت اعداداً اقل منها .

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ABBREVIATIONS

μE/m^2/s	Micro-einstein per square metre per second
μl	Microlitre
μs	Microsecond
ANOVA	Analysis of variance
ATP	Adenosine triphosphate
Candisc	Canonical discrimination
cm	Centimetre
diam.	Diameter
Fig.	Figure
ft	Feet
GC	Gas chromatoghraphy
h	Hour
hz	Hertz
ICIPE	The International Centre of Insect Physiology and Ecology
IPM	Integrated Pest Management
m	Metre
min	Minutes
nm	Nanometer
°C	Degrees Celcius or centigrade
r	Pearson's correlation coefficient
REGWF	Ryan's Q test or Ryan-Einot-Gabriel-Welsch-F-test

RH	relative humidity
rs	Spearman's correlation coefficient
s	Second
SAS	Statistical Analysis system
SE	Standard error
TL	Total length (from snout of lizard to tip of tail)
u-v	Ultra-violet
w/m^2	Watt per square metre

INTRODUCTION

Tsetse flies occur in Africa within latitudes circa 14° North and 20° South, on about 10 million square kilometres covering 31 countries where they put 50 million people and their livestock at risk of sleeping sickness. The 22 species of tsetse are separated into 3 groups (subgenera) based on the genital armature: fusca (subgenus *Austenina*), palpalis (subgenus *Nemorhina*) and morsitans (subgenus *Glossina* s. str.). All species of Glossina are susceptible to infection by trypanosomes - though unequally - but the forest species (Fusca group mainly) rarely come into contact with man and his livestock. The species that are considered to be the main vectors of human trypanosomosis are *G. palpalis* and *G. tachinoides* in West Africa and *G. fuscipes*, *G. morsitans*, *G. swynnertoni* and *G. pallidipes* in Central and East Africa (Okoth, 1986).

Curative and prevention methods have been used to manage tsetse for a long time. The high costs of drugs and the development of resistant strains of trypanosomes limit the effectiveness of medication against trypanosomosis (Jordan, 1986). Alternatives include the use of trypanotolerant breeds of cattle, sheep and goats; however this usually encounters a cultural resistance to small breeds of cattle. Vector control methods previously included clearing of vegetation and destruction of wild animals and application of insecticides in violation of the imperative to preserve the environment. Reinvasions of treated areas are frequent.

Due to increasing knowledge of the ecology, behaviour and physiology of tsetse flies, vector control is becoming more realistic. Environment-friendly methods include the use of traps and targets, with olfactory attractants and the release of sterile males to reduce tsetse populations to manageable levels.

The present work attempts to understand visual and olfactory cues that mediate host-location behaviour of a palpalis tsetse, *G. f. fuscipes* along Lake Victoria, Kenya.

Vision is critical in the Biology of tsetse flies. However, studies on visual cues for tsetse (Challier, 1982; Dransfield *et al.*, 1982 and Green, 1991) have shown that there are considerable inter- and intra-specific behavioural variations in tsetse flies (Green, 1993). The level of success of a trap varies according to tsetse species.

The biconical trap is now a firmly established visual trap for tsetse flies in several west African countries where it is efficient in capturing both the savanna species *G. m. morsitans* and the riverine *G. palpalis* (Muirhead-Thomson, 1991). Mwangelwa *et al* (1990) confirmed the superiority of this trap for *G. f. fuscipes* as compared to members of the Ngu-trap series which are more efficient for *G. pallidipes* (Brightwell *et al.*, 1987). The pyramidal trap was found virtually equal to the biconical trap in terms of catches of *G. f. fuscipes* (Mwangelwa, 1990 and Mohamed-Ahmed, 1992). The monoconical trap has been advocated in Uganda as well as the bipyramidal trap in the Central African Republic.

The operation of the biconical trap is based on the principle that tsetse flies tend to alight more on a black than on a blue cloth (Green and Flint, 1986). The latter elicits a stronger attraction (Challier *et al.*, 1977; Green, 1989 and Green and Flint, 1986). Hence, blue traps increase the catch by maximizing the attraction on the outside while the black inside stimulates the "entering" response (Wall and Langley, 1991). There is a consensus that visual stimuli act synergistically (or antagonistically) with endogenous factors and olfactory cues (Wall *et al.*, 1993).

Spontaneous activity of tsetse generally follows a diurnal trend, increasing after sunrise, decreasing during midday owing to high temperatures and then increasing again until sunset (Brady, 1972 and Allan *et al.*, 1987). This trend is generally true, except for some extreme cases like the crepuscular tsetse, *G. longipennis*.

It seems that *G. f. fuscipes* too is an exception and does not follow that generalized trend of diurnal activity. This species is active at the hottest and the brightest time of the day (1100-1400 h) (Mohamed-Ahmed and Odulaja, 1997). Its behaviour also suggests sex differentiation in light preferences, which is also reflected in biotope choices of males and females (Rogers, 1977) and in their succession pattern of diel activity. Females prefer brighter hours of the day (circa 1300-1400 h East African time), while males are more active at less bright hours (0900-1000 h) (Mwangelwa *et al.*, 1990).

An interesting host regularly quoted for *G. f. fuscipes*, is the Nile monitor, *Varanus niloticus* (Linnaeus 1766). This big lizard is distributed from South Africa North to Egypt in the East and Liberia in the West (Welch, 1982). Several workers (Weitz, 1963; Okoth *et al.*, 1990; Moloo, 1993; Mohamed-Ahmed and Odulaja, 1997 and Gouteux *et al.*, 1994) had shown through blood meals analyses that *V. niloticus* is an important host of *G. f. fuscipes*.

From the analyses, two schools of thought have emerged. One classifies *G. f. fuscipes* as a strongly opportunistic (generalist) bloodsucker for which availability of a host and its tolerance is the determinant factor. The other school of thought attributes to *G. f. fuscipes* a strongly selective host-preference in favour of the monitor lizard.

For Weitz (1963), the main hosts of *G. f. fuscipes* are Man (18%), bovids (38 %) and reptiles (34 %). Feeding on humans depends on availability, but there is a distinct attraction to man not so consistently displayed by other species of *Glossina*. The bushbuck is an important host where reptiles have been eliminated (20 %). In the Central African Republic, along riverine forests, 87% of the blood-meals of *G. f. fuscipes* are derived from wild ruminants (*Tragelaphus scriptus, Cephalophus sp., Kobus kob*). Blood meals from cattle (9-22%), from reptiles , *V. niloticus* and crocodiles (17-35%) and man (4-14 %) and suids (2-19%) were reported (Gouteux *et al*., 1994) in the neighbourhood of watering-places.

On the other hand, the Nile monitor was reported to contribute up to 90% of the total meals of this tsetse fly (Mohamed-Ahmed and Odulaja, 1997). While from the generalist school, the expectation could be that some generic tsetse attractants operate on such a diversified repertoire of hosts, from the opposite concept, cues that specifically emanate from the monitor lizard will be operational. However, less preferred hosts may produce varying amounts of such compounds, in part dependent on their diets and may attract *G. f. fuscipes*, albeit to a lesser degree. (Prof. Hassanali, pers. comm.).

Nevertheless, a host like the monitor lizard contrasts with some postulates that have been formulated for hosts of riverine tsetse (Davies,1977):

- very few favoured hosts of tsetse are smaller than the smallest antelopes, despite the fact that a great number of smaller animals may live in the tsetse habitat;
- antelopes are the favoured hosts of riverine tsetse; reptiles are just a substitute when antelopes migrate;

- Tsetse flies feed more on hosts that are resting in shade than in sunlight.

The initial attraction of *G. m. morsitans* or *G. pallidipes* is primarily mediated through endogenous rather than host stimuli (Torr, 1988; Vale, 1980; Bursell, 1970 and Madubunyi, 1995). Tsetse are known to be selective about their hosts (Galun, 1977 and Turner, 1987), with a certain degree of opportunism (Vale, 1977; Weitz, 1963 and Moloo, 1993). There is an agreement that host-finding involves some general blends (Willemse and Takken, 1994; Den Otter *et al.*, 1988) and some specific blends of attractants and stimulants or deterrents (Saini and Hassanali, 1992). The efficacy of odour-baited traps on *G. pallidipes* has become evident (Owaga, 1985; Owaga et al., 1988 and Dransfield *et al.,* 1986), especially cow or buffalo urine in conjunction with acetone on F3 or Ngu-traps. However, there is a shortage of information about it for *G. f. fuscipes*.

Mwangelwa *et al*. (1990) obtained contradictory results from one experiment to another when he tested the effect of cow urine on biconical traps for *G. f. fuscipes* on Rusinga island, Kenya. Gouteux et al. (1995) used a bipyramidal trap and increased the catch of *G. f. fuscipes* in the Central African Republic in the range 1.2-1.5 in six experiments and 2.2 times in one experiment. The catch index of males reached 4.2 in one experiment that was conducted in an area with low abundance of tsetse flies. These authors also used a varan in a box near the trap and increased the catch 1.7 times in two experiments, obtaining results similar to those from western Kenya by Mohamed-Ahmed and Odulaja (1997).

All the studies mentioned here suggest that in *G. f. fuscipes* host odours play a role in host location, even though no consistent improvement in trap catches have been reported using odour baits. Though, Filledier et al. (1988) had concluded that riverine tsetse depend exclusively on visual cues and on a waiting-strategy for their host-finding.

This study was conducted on *Glossina fuscipes fuscipes*, a riverine species of Central and Eastern Africa. It focuses on (i) colour preferences, ii) landing and feeding behaviours on a host, the Nile monitor and on (iii) the trappability in odour- and colour-baited traps.

Colour preferences were studied using electric screens in the field. Landing and milling-around behaviours were recorded for each colour tested. Spectroradiometer analyses allowed to define the reflectance of each colour from near u-v to near infra-red wavebands. The effect of reflectance at different wavebands (hue) on the attraction and on the landing of *G. f. fuscipes* was defined. Colour being an appearance of light, the detailed behaviour of *G. f. fuscipes* under changing light conditions was observed on the biconical trap and the Vavoua and the pyramidal traps to attempt an explanation on why the biconical trap usually predominates.

The usual significance of sites as a source of tremendous variation in experiments with visual traps and odours on *G. f. fuscipes* (Mwangelwa 1990; Oloo, pers.comm.; Mohamed-Ahmed, pers. comm. and Gouteux *et al.*, 1995) was also explored in terms of fly abundance and effects of rainfall.

Adaptive responses of *G. f. fuscipes* to the varans such as anemotactic flight, body zone preference and its dependence on temperature and light were investigated, using cage experiments and direct observations. The trends of feeding by *G. f. fuscipes* on the Nile monitor in nature were explored as well, using field binoculars. The compatibility of the diel activity patterns, co-occurence in the habitat and the repertoire of anti-tsetse behaviours of the lizard were investigated to confirm the fitness (availability and tolerance) of the monitor lizard as a host. Active compounds identified by laboratories of Chemical Ecology and Behavioural Biology at the International Centre of Insect Physiology and Ecology (Nairobi) were traced on different body zones of the monitor lizard.

Colours that were found most attractive were combined to make traps. These traps were tested as visual baits, compared to the standard biconical trap (Challier *et al.*, 1977). The performance of the most successful trap type was analyzed in relation with fly sex and fly abundance. It was baited with zebu urine at changing age of storage to estimate an optimum age of urine for baiting *G. f. fuscipes* traps in field conditions. Zebu urine was also tested in conjunction with acetone. Whole body odours and urine of the varan were tested as attractants too.

The fundamental questions raised were the following:

i) What is the colour preference of *G. f. fuscipes*? Which spectral characteristics of colours trigger such preferences?

ii) What are the sources of variation of the catch index when visual or olfactory stimuli are tried on *G. f. fuscipes*?

iii) If the host-finding of *V. niloticus* by *G. f. fuscipes* involves chemical cues, can it be proved through anemotactic experiments?

iv) Can *G. f. fuscipes* be seen feeding on *V. niloticus*, and which are the behaviours associated?

v) Can an innovative colour combination improve the efficiency of the biconical or pyramidal trap and perform better than the black conventional target?

vi) Can cow urine improve the catch of *G. f. fuscipes*? The interest of cow urine is high due to its availability in our villages.

2. LITERATURE REVIEW

2.1. Vectorial and socioeconomic importance of *G. f. fuscipes*

G. f. fuscipes has been implicated as the main vector of sleeping sickness epidemics in Eastern Uganda. Between 1976 and 1983, 10,414 male and 9,560 female patients in Busoga area had been infected with *Trypanosoma rhodesiense* (Abaru, 1985), reaching a total of more than 40,000 cases from 1976 to 1990. Katabazi *et al.* (1981) found an infection rate of 2.5% (labrum and hypopharynx) in flies netted on people in the field. Tsetse flies infected with *T. brucei* were caught at sites near water holes, homesteads and shambas (Okoth, 1986). This breeding in peridomestic habitats results in more intense contacts between man and fly even at very low fly densities (Okoth, 1986).

In Southern Sudan, *G. f. fuscipes* appears to be the sole vector of Gambian sleeping sickness in the Yambio area of western Equatoria Province; 9 of 14 blood meals were reported to be from man. As *G. f. fuscipes* is a poor vector of trypanosomes, and the pattern of human cases in this area is patchy, it was suggested that multiple infections may arise as a result of a single infected tsetse biting several people at the same watering place (Snow, 1984). The analysis of blood meals from the Nola-Bilolo focus of sleeping sickness in Central African Republic, showed that, unlike *G. p. palpalis*, *G. f. fuscipes* feeds more on men than on pigs. In the latter area, *Trypanosoma vivax* infection was observed only in *G. f. fuscipes* (Gouteux *et al.*, 1993). The same fly species is the main vector of bovine trypanosomosis in the area of the Central African Mbororo cattle breeders.

The vectorial capacity of *G. f. fuscipes* depends on the trypanosome stock. When *G. f. fuscipes* was fed on the flanks of Boran cattle infested with a *T. vivax* stock from Kenya, the mature infection rates ranged from 0-5%, as opposed to rates as high as 61-75% for *G. m. centralis* and *G. brevipalpis*. Rates were very weak in *G. austeni* and in all the 4 palpalis tsetse tested. In contrast, the hypopharyngeal infection rates of *T. vivax* from Nigeria were high in all 7 tsetse species and subspecies (55-97%) (Moloo *et al.,* 1987).

Adults of *G. f. quanzensis* captured at 2 sites in Brazzaville township (the zoo, downtown and on a farm in the outskirts) were infected with *T. congolense* (8%). The infection rates were higher in females (14% vs 5%). Maximum rates occurred in females at the age 20-30 days (Gouteux *et al.,* 1987). Trypanosoma infections occurred in horses and in dogs. All zoo animals examined in the area were negative for trypanosomes.

Control campaigns against *G. f. fuscipes,* alike other tsetse, require considerable investment and patience. An area of 2,000 km^2 in the Iganga District, eastern Uganda, was sprayed with deltamethrin at 0.2 g/ha from aircraft at intervals of 2-3 weeks (Ssebalijja, 1981). ORSTOM, the french overseas research organization, also started a control programme in Busoga, in 1987. Monthly treatment of cattle with pour-on deltamethrin supplemented the trapping with deltamethrin-coated pyramidal traps (Lancien and Coosemans, 1991). According to the late Lancien and Obayi (1993), traps (10/km^2) were impregnated with Glossinex (Deltamethrin, 300 mg a.i./trap) and covered an area of 3,000km^2 over 5 years. After 10 months, the *Glossina* population and the number of new cases of trypanosomosis was reduced by 90%. Over a 4-year period, the number of cases of sleeping sickness caused by *T. rhodesiense* fell from 6674 to 274 following the introduction of pyramidal traps for the control of *G. f. fuscipes*. The annual cost was 0.5 $/individual for the 600,000 persons (Lancien, 1993). The number of cases can increase if social disturbances interrupt health care and vector control (Okiria, 1983).

2.2 Motivation and pattern of tsetse movement

Tsetse exist at relatively low densities in the environment but combination of olfactory and visual stimuli brings males and virgin females together on or around host animals (Wall and Langley, 1993). It is also established that search for food, male's search for mating partners, female's search for larviposition sites and search for resting places (Laird, 1977) mainly motivate tsetse movement. In these regards, Bursell (1961) recognized four physiological phases of activity in relation to stages of digestion and fat reserves. He noted that along with the olfactory stimuli, temperature, relative humidity and luminosity are the main external factors.

It is believed that when tsetse fly about, there is a linear dispersal in the case of riparian populations and a surface dispersal in the case of savanna ones. In this linear dispersal, authors agree on the existence of preferred flight lines along open spaces, for example, paths and game tracks called "ecological corridors" by Gruvel (Laird, 1977). Brady and Crump (1978) showed that the 'v'-shaped activity pattern of *G. morsitans* is similar in field and in laboratory and that the zeitgeber is light intensity. The activity pattern was affected by temperature and physiological states such as hunger. They estimated that about 80% of the pattern of the field rhythm of *G. m. morsitans* is due to endogenous circadian clocks. The initial attraction of *G. m. morsitans* and *G.*

pallidipes is primarily mediated through endogenous rather than host stimuli (Torr, 1988).

Rogers (1977) observed a four day periodicity in recapturing rates of males of *G. f. fuscipes* suggesting a 4-day feeding cycle. Jack (1939) however stated that hunger is not the primary factor; and that flies are attracted to the points of greatest light intensity in the biotope. To locate a trap, a fly must be in its active phase (Laird, 1977). When Torr (1988) presented a moving target for 8 minutes, considerably more flies emerged from the refuge as compared with the numbers leaving when no light was visible; the percentage of different species and sexes responding was similar.

Vale (1980) discussed the importance of flight as a factor in the host finding behavior of *G. m. morsitans* and *G. pallidipes* and as a mean of encountering host stimuli in woodland and open areas and with mobile and stationary targets. He observed that flight can be initiated in the absence of external stimuli, especially when flies are in need of food and at times of day when flies appear at baits; this contributes to a mean daily displacement of several hundred meters in seemingly random direction (Bursell, 1970).

Oloo (1983) who studied the ecology of *G. f. fuscipes* at Gunga (Kenya) observed that light intensity was the key factor controlling the activity, with a peak observed at 10:45 at 20-26 °C. Mwangelwa (1990) caught no fly further than 100 m from the lakeshore. Willett (1965) observed *G. f. fuscipes* in areas away from rivers, particularly in *Lantana camara* thickets and in rings of vegetation surrounding villages in South Nyanza, Western Kenya. Okoth (1985, 1986) reported a similar situation in Uganda.

Rogers (1977) observed that there is an intermediate illumination at which the availability of male flies is at maximum. Both at lower illumination (belt of tall forest) and at high illuminations (patches of open grassland) catches of *G. f. fuscipes* were lower. Recaptures showed that movement was a simple diffusion from the point of release. Owaga (1981) cited Fiske (1920) who found that hunger increases the activity of *G.f. fuscipes* and this is manifested as a positive reaction to light, provided temperature is optimal.

Tsetse usually rest on lower branches of trees, except at temperatures above 36 °C when they exhibit a photonegative response (Jack and Williams, 1937) and enter dark refuges such as rot-holes in trees and antbear holes in the ground. They tend to have a strong photopositive response, which switches to a photonegative response when ambient temperatures exceed 30 °C. Immediately after larviposition females become strongly photopositive regardless of temperature (Allan *et al*., 1987).

Omoogun (1985) found that irrespective of zone and season, a temperature of between 26.1 and 26.7 °C appeared to favour a high density of tsetse in Egbe, Kwara State, Nigeria. Kyorku and Brady (1994) showed that *G. longipennis* readily flies in darkness and is even strongly inhibited during the light phase.

2.3 Colour preference by tsetse flies

2.3.1 Colour and reflectance

Visual trapping itself uses colours, and colours are known to be a resultant effect of light wavelength. In fact, the electromagnetic radiation emitted from the sun contains a band of frequencies characterized as gamma rays, X-rays, U-V (300-400 nm), visible light (400-650 nm) infra-red radiation (beyond 770 nm), micro-waves and radio-waves. Moonlight is low in intensity but has almost the same spectrum. Two characteristics of light can be regarded as qualitative properties: wavelength and the plane in which light waves are vibrating, the plane of polarization. In most insects visible light extends from about 300 nm to 650 nm.

Since the discovery by Karl von Frisch in 1949 of the use of the polarization plane of light from the sky in honeybee orientation, the capability has been found in many other arthropods, both terrestrial and aquatic. Fast eyes of rapidly flying diurnal insects such as bees and flies may resolve flicker frequencies as high as 265 per second (Marler and Hamilton III, 1966).

2.3.2 Traps and targets for tsetse flies

Targets and screens were developed in both Zimbabwe and West Africa for tsetse sampling and control. These consist principally of a central insecticide-covered cloth usually about 1 m in area. The face of the cloth is at right angle to the wind direction, presenting the maximum visual target for flies approaching from upwind. In addition to the visual component, an invisible flanking net was subsequently incorporated (Wall and Langley, 1991). Gouteux and Noireau (1986) tried an insecticide-impregnated model with intersecting blue and black screens with a plastic roof to protect from rain. It was as efficient as a biconical trap for *G. f. quanzensis* and *G. p. palpalis*.

Preferred target colours in the laboratory are black, blue and red; very few landings were observed on white and yellow (Green, 1991). During standing catches, electric screens - devices with electrified wires which electrocuted landing flies - are not markedly superior to the catch by measuring hand nets, but with moving catches the electric traps on average catch higher numbers of both males and females of *G. palpalis* and *G. tachinoides* (Muirhead-Thomson, 1991).

Turner (1987) found no significant difference between trapped and electrocuted *G. pallidipes* in terms of pregnancy condition and age structure. Traps were relatively more effective in catching males than females by a factor of 1.4.

Green (1986) studied trap responses of *G. palpalis* and *G. tachinoides*. He found that to perform well on a biconical trap, a colour must attract flies without inducing landing e.g phthalogen blue, but low landing is observed when used on screens. Any cloth used in combination with phthalogen blue for screens should be strongly reflective in 300-490 nm. But the relative attractiveness of black, blue and white depend on the species, the type of trap and the placement of colour on the trap (Challier, 1982 and Dransfield *et al*., 1982). In the same logic, Jordan and Green (1984) concluded that the most important colour determinant of trap score is the proportion of attractive blue (400-500 nm) to unattractive green-yellow (500-600 nm) in the reflectance of the material used. With materials strongly reflecting UV, a high proportion of flies, especially females, land (Jordan and Green, 1983). Reflectivity of red (above 600 nm) is also a positive factor in trap attractiveness.

Practical interpretation of field data is usually made difficult by inconsistency and failure to relate colour to objective physical standards (Jordan and Green,1983). Optimizing the visual attractiveness of targets is particularly important if odour is not employed to affect the initial attraction of tsetse to their vicinity.

Turner (1987) observed in Lambwe valley (Kenya) that the behavioural responses of *G. pallidipes* to colours in the field are complex. In general, trap effectiveness depends mainly on reflectivity from four different wavebands: blue-green and ultraviolet correlate positively with trap performance and green - yellow - orange negatively .

2.3.3 Effect of shade and shape on the attraction of tsetse flies.

Green (1989) stated that, because of differences in the biology of riverine and savanna tsetse species, workers in west Africa have concentrated on developing the visual attractiveness of traps, while those in East and Southern Africa have been particularly concerned with odour bait technology. These two approaches are now coming together.

The preference of unmated females and males in the laboratory for landing on vertical surfaces and borders of visual contrast is believed to be related to the innate alighting and resting behaviour. Pregnant females, however, show strong preferences in the laboratory for landing on horizontal surfaces, simple and unbroken areas and subterranean cavities (Allan *et al.*, 1987). Pregnant females show no preference for substracts of particular colour in the laboratory. The colour most attractive to host-seeking tsetse is blue followed by black and white. Of interest, are findings that the brightness of white cloth used for traps correlated with the number of insects collected (Allan *et al.*, 1987).

Tsetse are more attracted to uniform black targets than targets with numerous or complex edges such as strings. Increasing the size of moving or stationary targets increases the alightment response. High sensitivity to contrasts permits tsetse to detect distant objects (Allan *et al.*, 1987). The preference insects exhibit for particular shapes is related to the complexity of outlines: the more complex the contour, the more attractive a figure proves to be.

No consistent differences in ages and nutritional states were found between tsetse caught by coloured targets, but those landing directly on the cloth portion of target had lower fat reserves than those intercepted on an adjacent netting panel. The positioning of a strip of black against a white (painted) background optimized target efficiency on *G. pallidipes* (Green, 1988). Impregnated targets are black to maximize the landing response.

The best traps are those that provide a shaded area in such a way that tsetse attracted from far may mount into the lighted parts of the trap (Laird,. 1977). The trap must be sighted in such a way that all day it makes a marked contrast with its environment. During the dry season, high catches are expected because natural shade is reduced; flies look for shade in traps. Laird (1977) noted that large traps are better perceived from distance, except for *G. palpalis* and *G. tachinoides*.

It is hypothesized that, based on the tendency of *Glossina* to move towards dark surfaces and shaded cavities, the body of a trap is mistaken for a belly of an animal. Thus, many of the most effective types of trap were roughly the size and shape of a goat or small antelope and it was assumed that this resemblance to a potential host was the basis of the attraction of the fly to the trap. Once in the cavity of the trap, tsetse flies find themselves in a dark environment; then they are attracted toward the lighted summit of the trap (Laird, 1977). Inside the trap, the strongest light stimulus comes from above, through the mesh cone and as a result, once inside the trap flies tend to move into the collecting device at the apex (Wall and Langley, 1991).

Challier and Laveissière (1973) observed that the number of tsetse caught increases when traps are located at more open and even sunny locations. Swynnerton (1933) was of the opinion that the best year is when flies look for shade in traps (Laird, 1977).

Vale (1982) showed that a substantial proportion of attracted flies circumnavigate a trap or target within half a meter. The efficiency of targets, therefore, is generally higher than that of traps. Mesh flanking-nets either side of a target exploit this behaviour since the mesh is almost invisible to the approaching flies, which collide with it and come into contact with the insecticide (Wall and langley, 1991). Dransfield (1984) estimated the range at which a biconical trap could be detected to be 10-15 m for *G. brevipalpis* and 15-20 m for *G. pallidipes*.

The pyramidal trap was found to be more efficient than the biconical on *G. f. fuscipes*, especially when set at watering points in the Central African Republic (Gouteux, 1992 and Blanc *et al*., 1991) or impregnated with deltamethrin (Lancien, 1990) in Uganda. But the concentration of *G. f. fuscipes* is negligible at drinking places during the rainy season (Cuisance *et al*., 1991).

To improve the previous trap scores. Okoth (1991) designed a low-cost monoscreen trap for *G. f. fuscipes*, suitable for use by rural communities in Uganda. The trap comprised of a single blue-black screen and cone made from mosquito netting and it was 1.25 times as efficient as the biconical trap; however, the too high proportion of flies which circumnavigate or alight and fly away without entering remains a big constraint to tsetse trapping.

2.4. Host-finding by tsetse

Many facets of tsetse behaviour have been substantiated, either by direct close observation or at a distance with the aid of a telescope. By following a number of tame animals it is possible to record tsetse alighting or engorging on different body regions, and even to follow the movements of individual flies which alight several times on the same animal (Muirhead-Thomson, 1982).

2.4.1 Responses at long-range and anemotactic behaviour

In the opinion of Willemse and Takken (1994), four stages are recognized in the host-locating behaviour of flying insects: ranging, activation, orientation, and landing. The stimulus which evokes approach in daylight usually seems to be the visual one of host movement. At night, a positive anemotaxis triggered and maintained by olfactory stimuli, seems to be more important than visual stimuli in guiding certain insects to their vertebrate hosts (Galun, 1977).

Willemse and Takken (1994) estimated that 80% of the flies leaving an odour plume in a cross-wind direction turn sharply but without regard to wind direction, whereas 60% of flies entering an odour plume turn upwind. But, in typical tsetse habitats (e.g) in Rekomittje, Zimbabwe, wind speeds are low and the wind commonly changes direction at the rate of 5-20 deg./s; So Bursell (1984) assumed that under such wind conditions host location by upwind anemotaxis might be difficult.

Vale (1980) observed that 80 to 100% of flying tsetse responded to the host stimuli they encountered while flying into and out of woodland clearing. Jordan and Green (1984) stated that host-oriented responses of *Glossina spp* are directed partly by the movement of the animal and partly by its smell.

But, odour-guided host location is more important among savanna tsetse species than among the riverine ones (Filledier et al., 1988). Odour might be of little use in riverine habitat because it passes out of the forest if the wind is blowing perpendicularly to the forest edge. Tsetse following such an odour trail might waste energy, because it would not lead them efficiently to the host animal. A better way for this tsetse to find the host would be to fly over the waterline until an animal crossing or drinking at the site is reached (visual cues). In fact, Green and Cosens (1983) had shown that tsetse flies sit strategically; They favour horizontal branches 1-4 inches diam. The fly hangs from underside of a branch with the head pointing downwards along it, such a position affording the insect a maximum field of view..

Long-range attractiveness of an animal seems to be determined largely by weight rather than species. This suggests that long-range olfactory responses appear to be triggered by kairomones that are similar for most host species (Willemse and Takken, 1994).

Vale (1980) observed that the final stage of locating stationary hosts depends largely on upwind flight in response to host odour which, in the case of ox odour, forms a plume that extends effectively for about 90 m. However, he recognized that little is known of the circumstances under which upwind flight is initiated or the means of navigation in the plume. Flight can also be initiated in the absence of external stimuli, especially when flies are in need of food. Ranging in search of a host is an important strategy (Vale, 1977).

2.4.2 Responses at close-range

Muirhead-Thomson referred to studies in the 80s conducted on cattle which were either tame enough to allow the observer to approach and net flies as they landed, or at least sufficiently tame to allow an observer to stand for long periods at a distance of 10-15 ft, the identification of landing species being assisted where necessary with the aid of binoculars. In the choice of animal host for these experiments, no difference was noted between the attraction of animals of different colours by Tabanids.

Galun (1977) divides the blood-sucking process into four successive steps: attraction to the host and settling (orientation); probing and tasting (initiation of feeding); and withdrawal of mouthparts (termination of feeding). First, there must be active movement towards the warm-blooded host guided by visual and thermal stimuli emanating from the host.

Though generally variable in detail, the chemical stimuli conform to a common general pattern and are dominated by carbon dioxide, water vapour, fatty acids and their derivatives (especially lactic acid), ammonia and amines. The biting behaviour is conditioned mainly by visual and olfactory stimuli. Galun (1988) reported that the ability of *G. tachinoides* to detect ATP is the highest recorded so far among insects.

Goes van Naters et al. (1993) provided electrophysiological evidence that for *G. f. fuscipes* human sweat is an adequate stimulus. The receptor cells which respond to human sweat are located in two sensillae proximal to the base of the empodium at the distal end of the fifth tarsomere. The receptors are sensitive to 4 of the 14 major components of sweat tested: uric acid, leucine, valine and lactic acid. It is shown that flies display more feeding on surface treated with sweat, uric acid, leucine or valine than on untreated surfaces. Although there is some evidence of the existence of close-range olfactory cues such as lactic acid (Vale, 1979) and sebum (Warnes, 1989; 1990) no studies have yet been undertaken to examine whether such cues influence the feeding choices of tsetse.

On the other hand, there are indications that at close range the host species produce distinctive kairomones from their skin that may cause differences in the alighting responses. Willemse and Takken (1994) quoted Warnes (1989, 1990) who had shown that low volatility skin products, such as lactic acid and ox sebum, affect feeding success and behaviour after alighting but have no effect on the alighting behaviour.

Other aspects of odour that affect the alighting behaviour are concentration gradients. When visual targets are presented, odour gradients tend to increase the proportion of flies that alight on or land near the targets as observed by Bursell (1990). Willemse and Takken (1994) indicated that near an odour source, tsetse divert to visual objects. The percentage diverting depends on visual aspects (size, shape, colour) but not on composition of the odour or loss of contact with it. Some important stimuli from man are visual; the movement of man may account from a distance, whereas the upright form of man may be a close-range repellent (Vale,1979).

Marler and Hamilton III confirmed that the stronger the stimulus the longer the bout of feeding of flies, feeding bouts lasting on average from 51 to 133 seconds, depending on the length the animal had been deprived of food. The effect of blood compositions on host discrimination, i. e. the presence of proper phagostimulants in the diet is very important as shown by Galun (1977).

2.4.3 Tsetse attractants

Since tsetse are known to be selective about their hosts, host-finding may involve specific blends of attractants and stimulants or deterrents. Considerable progress has been made in identifying such kairomonal compounds that mediate the host-seeking behaviour. These compounds form part of the excretory products of host animals and include breath volatiles like carbon dioxide, acetone, butanone and 1-octen-3-ol (Vale and Hall, 1985) and urine phenols comprising the parent phenol, 3- and 4-cresol, 3- and 4-ethylphenols, and 3- and 4-n-propylphenols of which 4-cresol and 3-n-propylphenol have been found to be crucial compounds (Okech and Hassanali, 1990). These compounds are either emitted by the hosts themselves or as part of airborne volatiles of their excretory products (Saini and Hassanali, 1992).

Thermal stimuli are important in attracting ticks, bugs, lice, mosquitoes and tsetse flies to their hosts. The importance of a warm upward current of air for host-finding was demonstrated for ticks, blackflies, fleas and mosquitoes. Neither CO_2 nor visual or thermal stimuli could account for any host specificity. A single blood-sucking species may be polyphagous and feed on several species of reptiles, birds, or mammals (Galun, 1977).

The scent of elephant dung and urine attracts *G. morsitans* Westwood and that of excreta of buffalo, cattle and hippopotamus, *G. pallidipes* Austen. Hippopotamus odour was also attractive to *G. palpalis fuscipes* Nestead (Den Otter *et al.*, 1988; Chorley, 1948) . Mohamed-Ahmed et al (1992) found a similar preference in *G.f.fuscipes* of Western kenya. The studies of Den otter (1988) did not show any difference in the response of 5 tsetse species to acetone, 4-heptanone, 3-nonanone and octenol. It suggests that these compounds do not determine host preference.

Attractive components of odour are exhaled by the host. So, they are released discontinuously (Vale, 1984). Willemse and Takken (1994) noted that for tsetse, visual cues, including contrast, shape, and colour, are important in host location at short range. However, tsetse are also able to locate hosts from much greater distances that are not visible to them. Tsetse could employ two different policies in their overall strategy of host-location: ranging in search of hosts and waiting for passing animals (Vale, 1980).

2.4.4 Host preference by tsetse flies

Tsetse land and feed selectively on their hosts. Galun (1977) postulated that in the face of competition from other parasitic species, the polyphagous parasite will have a higher survival rate on those hosts on which it is a more successful competitor. Animals avoided by tsetse flies include duiker, waterbuck, Grant's gazelle, impala, hartebeest, zebra, baboon and dikdik. Lamprey et al. (1962) studied a system where the impala accounted for about 70% of mammals in the area, yet they contributed only for 1% of the meals of *G. swynnertoni* while the relatively scarce warthog contributed 77%.

Turner (1987) found no relationship between the relative abundance of different vertebrate species and the frequency with which they were fed on by *G. pallidipes*. Impala, obi, water buck were common in Lambwe valley (Kenya), but not fed on or hardly fed on (reed buck, hartebeest). 70% bloodmeals were from bovids with 57.1% from bushbuck and Buffalo, 25.6% from suids (bushpig), duiker (7.6%)

and 4.2% from primates, probably man. Monitor lizards contributed 10.4% for samples from the thicket only and 0 % in woodland.

Okoth and Kapaata (1990) investigated the host preferences of *G. f. fuscipes* in a peridomestic situation and on Lake Victoria, Uganda; 73 feeds (24%) came from reptiles (mainly *Varanus spp*) 4 (1.3%) from birds, 82 (27%) from primates (including man) 3 (1%) from suids (*Potamochoerus porcus*) and 138 (44.4%) from bovids (including *Tragelaphus scriptus*). In a peridomestic situation, 41 feeds (19.3%) were from reptile, 4 (1.9%) from birds, 69 (32.4%) from primates. 45 (20.2%) from suids and 55 (25.8%) from bovids.

Hosts favoured by many species of *Glossina* belong mainly to the family *Suidae* and *Bovidae* (Galun, 1977). The discrimination of tsetse flies in favour of certain hosts is a reflection of a coincidence of the habits of the fly and the host. Nash (1969) assumed that host selection depends on "the reliability" of the host species. Provided the species is reasonably attractive, tsetse flies feed more often on one which has reliable habits. Fatness of hosts and thickness of their fur and evasiveness may also play a role in causing the flies to be reluctant to feed. Simpson's observation (Nash, 1969) showed that even when monkeys appeared to sleep when a fly settled on them, they either caught and ate it, or they frightened it away. Vale (1977) observed that the proportion of fed *G. pallidipes* and *G. morsitans* fell by 1/3 when the number of flies attracted to the ox had increased to a point that the ox became intolerant.

Thus, it is clear that recent studies have emphasized the importance of stimulus interaction during the process of host- finding and host acceptance by insects. Several authors (e.g. Aluja and Prokopy, 1993; Torr, 1988, Brady *et al.*, 1989; Harris *et al.*

1993 and Gibson *et al.* 1991) share that opinion. However, there is a tendency to generalize that stimuli for long-range recognition and for short-range attraction are respectively similar or non-specific for different species. This view can mislead the interpretation of behavioural differences which are accepted as a fact. It is shown, at the same time, that much remains to be explained in host-finding mechanisms of tsetse.

3. MATERIALS AND METHODS

3.1 Colour preferences of *G. f. fuscipes*

Experiments were conducted mainly on Rusinga Island, Kakrigu village (Plate 1), Western Kenya, and partly in Kisui village 10 km away on the mainland. The island occupies an area of 43 sq km and it is situated on longitude 34° 10' E and latitude 0° 25' S. At lake Victoria level, it lies at an altitude of 1128 m and receives a mean annual rainfall of 1060 mm and a strong sunshine (Fig. 1). According to the ecological classification of Pratt et al. (1966), the area would fall under zones IV/V.

3.1.1 Vegetation and animals in the study area

Fields near the lakeshore are demarcated with fences of *Euphorbia tirucalii* (L.) or *Lantana camara* (L.). *Ficus spp.* are scattered in the agroecosystems. Maize, sorghum, cassava, bananas, sugar cane, sweet potatoes and vegetables are grown. Several shrubs occur in virgin lands further from the Lakeshore : *Triumfetta macrophylla* (K. Schum), *Mimosa pigra* (L.), *Phichea ovalis* (Pers) and *Ipomea hilderbrandtii* Vatke (Mwangelwa *et al*., 1990).

Strictly at the shoreline ecotone habitat, the tree species *Sesbania sesban* (L.) Merrill and the ambatch, *Aeschynomene elaphroxylon* (Guill and Perr) Taub. dominate, in association with *Phragmites* and creepers of the family *Nyctaginaceae* and also the genus *Ipomea*. Sedges, *Cyperus immensus* (C.B.Cl.) and *C. articulatus* (L.) are also frequent. Water hyacinths are common at specific sites during the dry season and harbour large monitor lizards (*Varanus niloticus niloticus* Laurenti) if dry trunks of *Aeshynomene* are not available for basking.

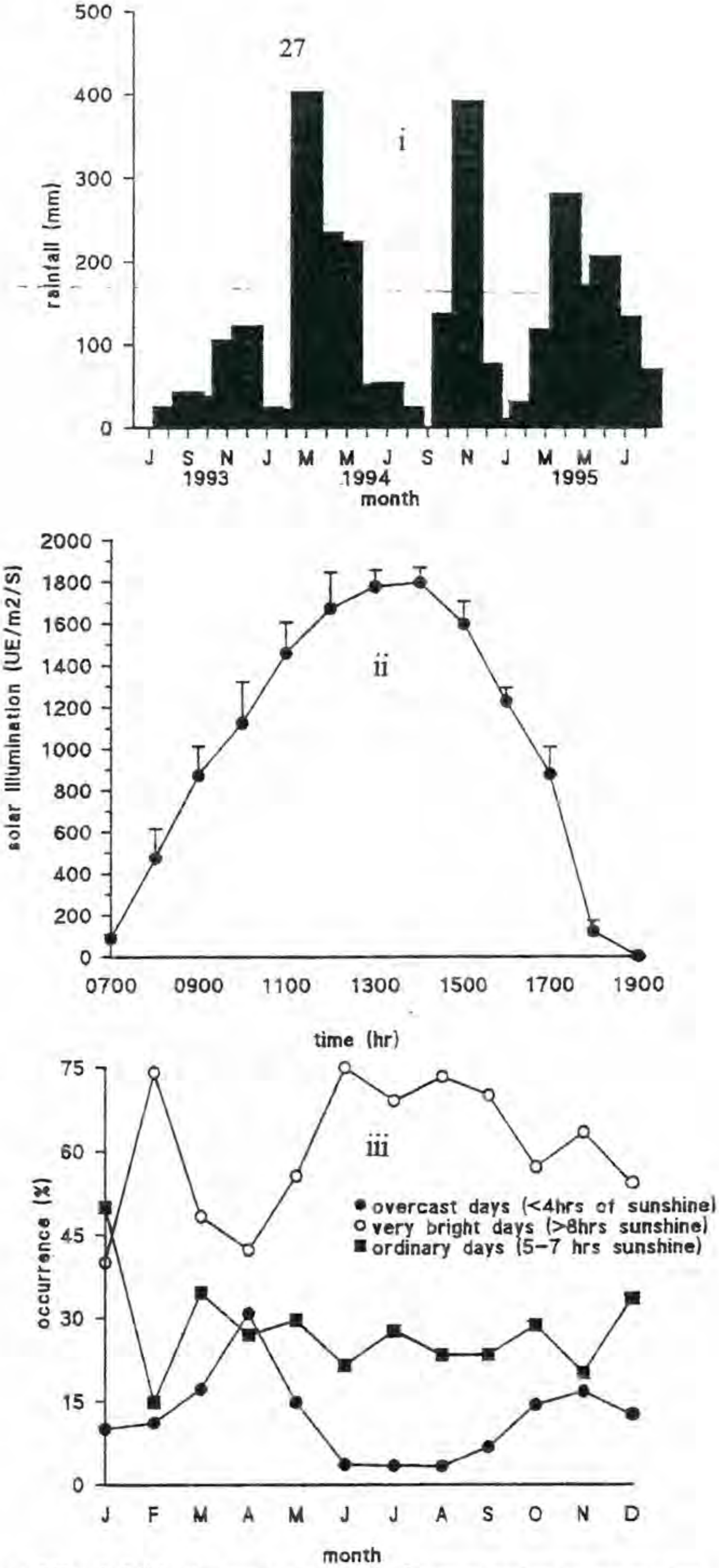


Figure 1: Pattern of (i) rainfall in the study area (ii) solar illumination by sunny day ($n = 30$) and (iii) estimated proportion of sunny and overcast days per month, based on heliograph values. Computation of data from ICIPE Mbita Point meteorological station.

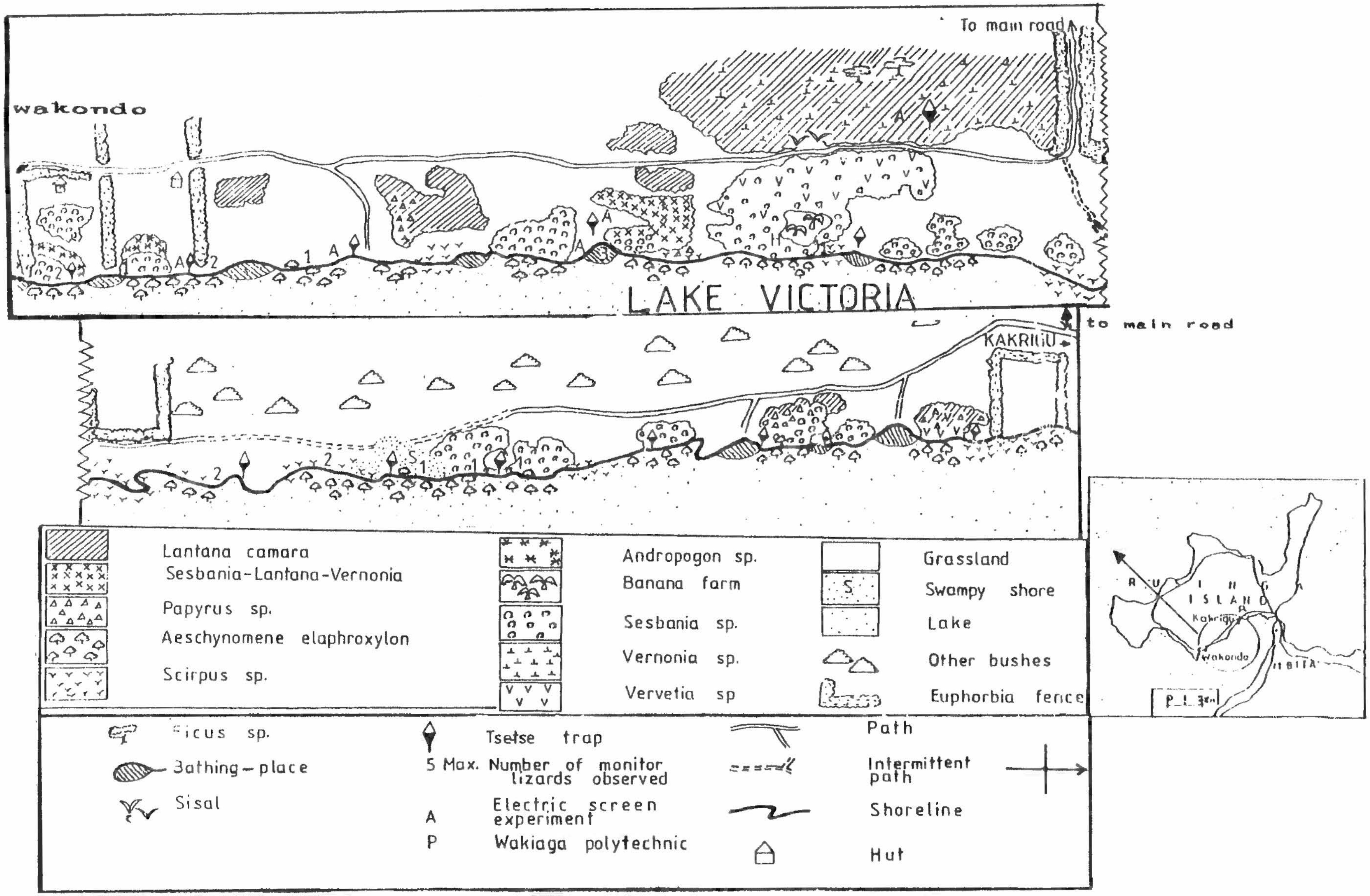


Plate 1: Diagram of the various vegetation communities and location map of the main trapping sites during this study on Rusinga Island, Lake Victoria.

At the site where most of the electric screen experiments were run, *Sesbania sesban* was tall and dominant with *Aeshynomene* underneath. Wood trunks of *Aeschynomene* dominated the littoral. *Andropogon spp.* colonized the background. At a site where the red colour combinations were tried, near a resting site of hippopotamus (*Hippopotamus amphibius* Linnaeus 1758) with a huge hippo dung on a corridor 100 m from the shoreline, there is a bush of *Sesbania sesban* with *Lantana camara* as undergrowth and Vernonia sp. on the margins.

The trapping experiments conducted at the farthest point from the lakeshore (ca. 200 m) took place in a dense shrub dominated by *Vernonia sp.* and *Lantana camara* with some scattered *Ficus sp.* on which 6 monkeys (*Cercopithecus albogularis* Sykes 1831) were sometime observed. The lake side just across the road (corridor) was dominated by *Sesbania sesban* with *Vervetia sp.* and a banana field.

This seems to be the main hippo refuge at breeding times (footprints, dung, daytime occurrence with a kid). Some porcupines (*Hystix africae australis* Peters 1852) were observed in this biotope. Most trapping experiments were conducted just at the shoreline. At a site quoted no 8 at open lakeshore, there was scattered *Sesbania sesban* and *Andropogon sp.* at the margins on the lakeside; Vernonia sp. and *Lantana camara* with *Sesbania* were associated in the background.

Site no 7 comprised of a denser shrub with the ambatch in water and *Sesbania* just next on land. Site no 6 was a water-logged swamp with the ambatch dominant and with *Sesbania* off swamp. Water hyacinths were abundant and lianas covered the ambatch. Sites no 3, 4 and 5 were bushes of ambatch and lianas and *Aspir sp.* Site no 2 was colonized by an association of *Aeschynomene-Sesbania-Lantana* and reeds and

Papilonesi sp. Site no 1 was dominated by big trees of *Sesbania* at the lakeshore and a thicket of *Lantana*-reeds-*Vervetia*. Only here, *Scirpus* was observed in water 5 m from the lakeshore. Bathing places were scattered all along the shoreline. Cattle and goats were brought for drinking; People searched for worms (fishing-baits) in swamps.

3.1.2 choices of colours in the field

Electric screens with 130x115 cm frames painted matt black were used. They carried 8-mm-spaced high tension wires across. They were used to mount 50 cm of coloured cotton fabric flanked with 25 cm of black netting either sides.

A single colour or a colour combination was set on each screen between the two parallel series of wires (Fig. 2). The electrocuting-grids were powered by a 12 V car battery driving an inverter-transformer oscillator generating spikes of > 25 kV lasting ca. 250 µs, discharge frequency 67 Hz; 0.018 coulombs (Griffiths et al 1994). Batteries were tested for voltage in the morning after charging over night.

The screens were set at selected sites with dense tsetse populations. Multiple-choice designs were used (Griffiths et al 1994; Bracken & Thorsteinson 1965). Two screens were set for two-choice experiments, and three screens were used for three-choice experiments. Positions of colours were changed at each replicate in the twos or the triplets following the order A-B, B-A or A-B-C, B-C-A, C-A-B. Four to six replicates were done for each experiment. A distance of 30 cm separated any pair of screens. The blue/black combination (score = 1.0) was used as a control at each trial. When one screen underwent an interruption, the whole set was discounted. This was to control the effect of position at each site.

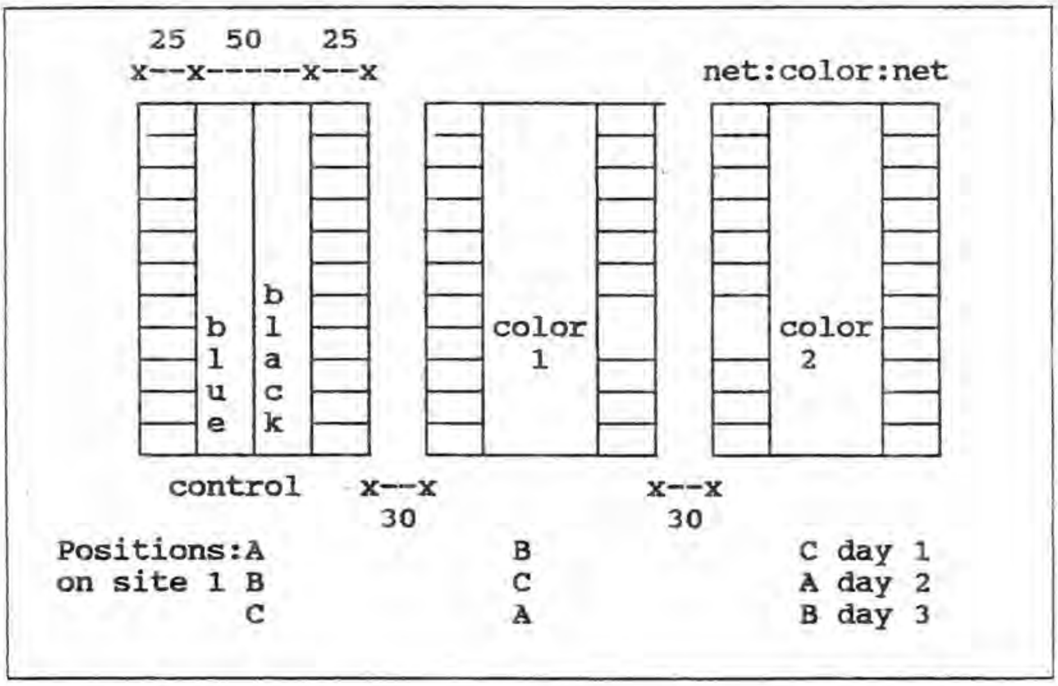


Figure 2: Experimental setup for electric screens in the field. Three screens were used during each experiment. The blue/black screen was used every time as a reference. Only the test involving blue vs red involved two screens. Targets were shifted according to a 3x3 latin square design (n = 5-6). All screens were positioned at a similar angle such that tsetse flying upwind would approach them with a similar chance. Distances in cm.

The sampling time was between 1000 h and 1400 h which is the range of the peak activity of *G.f.fuscipes*. Each session was running for three hours to avoid exhaustion of the car batteries. The buzzing sound of the sparking on the wires allowed us to judge whether a screen was still running. Very short visits at the site were made hourly to ensure that the system did not stop. Experiments were carried on only by sunny days when flies are active, and also to reduce the variation of reflectance.

Flies caught on the sticky iron-sheet just below the cloth represented the "landing" component of the catch. The catch below the flanked black netting constituted the "spinning" or "milling" component of the sample. The sum of both components is the total approach to a given colour or colour combination. The flies electrocuted on electric screens were sexed and counted.

3.1.2. Measurement of the reflectance of the experimental cloth fabrics

The portable spectroradiometer Li-Cor Li-1800 was used to measure the reflectance of the experimental cloth fabrics. The scan limits extended from 300-850 nm. The scan interval 2 nm was chosen, with 3 scans simultaneously. The presence of the incorporated calibration files was verified. The illuminator lamp was allowed to warm up at least 30 seconds before taking any data. The sphere ports A and B was attached to a standard camera tripod to maintain the ports horizontal to avoid illuminator output variations due to the orientation with respect to gravity.

The output gave the reflectance (% as compared to Barium sulfate) which resulted from the ratio Rs = Is / Ir:

where Rs = reflectance of the sample

Is = sphere output when the sample is measured

Ir = sphere output when the reference material, barium sulfate, is illuminated

3.1.3. Measurement of the irradiance of the cloth fabrics

The portable spectroradiometer Li-Cor Li-1800 was used to measure the irradiance of the experimental cloth fabrics. The blue (450-490 nm) and the near infra-red (750-850 nm) ranges of the spectrum were selected for the measurement of the quantum reflectance of the experimental cloth fabrics and of skin samples from the neck, the back and the leg of a Nile monitor. The selection of the above wavebands was based on previous results showing that a given colour's intensity of landing and spinning is strongly related respectively to its reflectance in the blue and in the infra-red ranges.

Each sample was scanned 4 times from 390 nm to 850 nm, yielding a separate file for each experimental colour. The spectral integration (IT) was performed within each file over the blue and the infra-red wavebands. The output irradiance value of the waveband was divided by the wavelength range, respectively 40 for the blue and 90 for infra-red ranges. Mean values were, thus, obtained in watts/m^2/nm. The Quantum integrate function (QI) was also used to apply a quantum transformation and estimate the quantum flux density over the given wavelength ranges.

Correlation between reflectance values and flies caught in the field. Means of the reflectance within each spectral class were obtained by computing the average of all the values at 10 nm interval from the first 2-nm-scans; e.g. the reflectance (%) at 450 nm, 460 nm, 470 nm... in the blue spectral class. Means of the reflectance within each spectral class were correlated (Pearson's r) with the average field catch of each colour, respectively for "attraction" and for "landing". The purpose was to estimate the effect of hue on each of the 2 behaviours of the fly (i.e the potency of the colours on the targets to attract or to elicit the landing. Multiple comparisons of means were done using Ryan's Q test (Day & Quinn 1989) after arcsine transformation (SAS, 1987).

3.1.4. Terminology used and interpretation of the wavelength basis of the colour choices (Allan & Stoffolano 1986)

Colour is generally considered to have 3 attributes: hue, saturation and intensity. Hue is defined by the dominant wavelength, i.e., violet (380-450 nm). A chromatic colour possesses a hue, i.e., blue; an achromatic colour is one without a hue, i.e., white or grey. Saturation is based on the proportion of pure chromatic colour (i.e., pure pigment). When white is added to a colour, the colour becomes unsaturated.

Data of reflectance (%) at the different wavelengths were classified as follows: violet (380-450), blue (450-490 nm), green (490-560 nm), yellow (560-590 nm), orange (590-630 nm), and red (630-760 nm) in accordance with Allan et al (1986) and infra-red from 760 to 10exp6 nm (Callahan 1965). In this case, only the near infrared range was scanned within 760-1100 nm as allowed by this spectroradiometer.

The intensity of the landing behaviour (%) on a given colour was interpreted in comparison with the landing on the blue/black standard. The milling behaviour around the target (catch on the flanked invisible netting) was interpreted as the attraction.

Means of the reflectance within each class were regressed with the average landing, milling catch to estimate the effect of hue on each of the given behaviour of *G. f. fuscipes* (i.e. stimulation of landing or attraction by the colours on the targets). This procedure was adapted from Jordan and Green (1983).

3.1.5. Identification of the experimental colours

The nomenclature of experimental colours (Plate 2; Table 1) was done according to the Horticultural Colour Chart of the British Colour Council and The Royal Horticultural Society (Wilson, 1938) and the Rock-colour Chart of the Geological Society of America (Goddard et al. 1963) for dark colours.

3.1.6. Approximation of the sensitivity curve of *G.f.fuscipes*

Owing to the difficulty to run the appropriate phototactic and electroantennographic experiments, especially involving the invisible range (ultra-violet and infra-red), the sensitivity curve was estimated using the intensity of the relation between each class of wavelength and the intensity of the landing or of the attraction (r-square such that negative Pearson's r in case of repellency or positive r in case of attraction are not shown). Two separate hypothetical curves were thus yielded respectively for the landing-behaviour and the attraction.

3.1.7. Distribution of G. *f*. *fuscipes* and rainfall as a factor of its dispersal

Eight biconical traps were set in the field. Catches were recorded every 24 hours. When an episode of rainfall occurred, catches of the successive days after the rain were compared to catches of the days before that rain (T-test). Taylor's power law was used to assess globally the distribution pattern of *G.f.fuscipes* (relationship mean-variance) .

Plate 2: Nomenclature of the experimental colours according to the Chart of the British Colour Council (Wilson, 1938). Code numbers indicate hue and chroma.

* identified according to the Rock-colour chart (Goddard et al., 1963).

Table 1: Common names used for the experimental colours and their nomenclature according to the Chart of the British Colour Council (Wilson, 1938) . * indicates designation from the Rock-Colour Chart (Goddard et al.). Code numbers indicate hue and chroma.

Name used	Identity in the colour chart
1. Violet	Amethyst violet
2. Royal blue	Princes blue 745/3
3. Green	Jade green 54
4. Yellow	Sulphur Yellow 1/1
5.Orange	Vermilion 18
6. Red1	Turkey Red 721/3
7. Red2	Peony Purple 729/1
8. Red3	Doge Purple 732/1
9. White	-
10. Brown	Grayish Brown (5 YR 3/2*)
11. Black	-

3.1.8 Detailed behaviour around traps

A trap was set and the behaviour of the flies around it was monitored through 10x50 field binoculars from a distance of ca. 20 m behind a bush for hiding and shade. The data were kept on a record-sheet (Martin and Bateson) (light, ambient temperature, time, landing-zones, numbers of responders per behaviour pattern) during continuous sessions of 120 minutes.

Solar radiation was measured in the field using a portable radiometer Li-Cor, with a quantum sensor Li-190sz. It measures the photosynthetically active radiation (PAR) in the 400 to 700 nm waveband. The unit of measurement is the micromole per second per square-meter (1 μmole/s/m^2 = 6.02*10exp17 photons = 1 μE/s/m^2). Full sun plus sky is approximately 2,000 μE/s/m^2 (Li-Cor, 1991).

3.2. Responses of *G.f.fuscipes* to a host, the Nile monitor

3.2.1. Experimental animals and biological parameters

Monitor lizards were trapped along the Victoria shore using fish-baited hooks. Animals were kept in a cage (66x48x189 cm) and given tap water every day. Lizards were weighed. Specimens which could accept food were provided with young Nile perch after 2 weeks of captivity. Animals were released to the wild after three weeks of use.

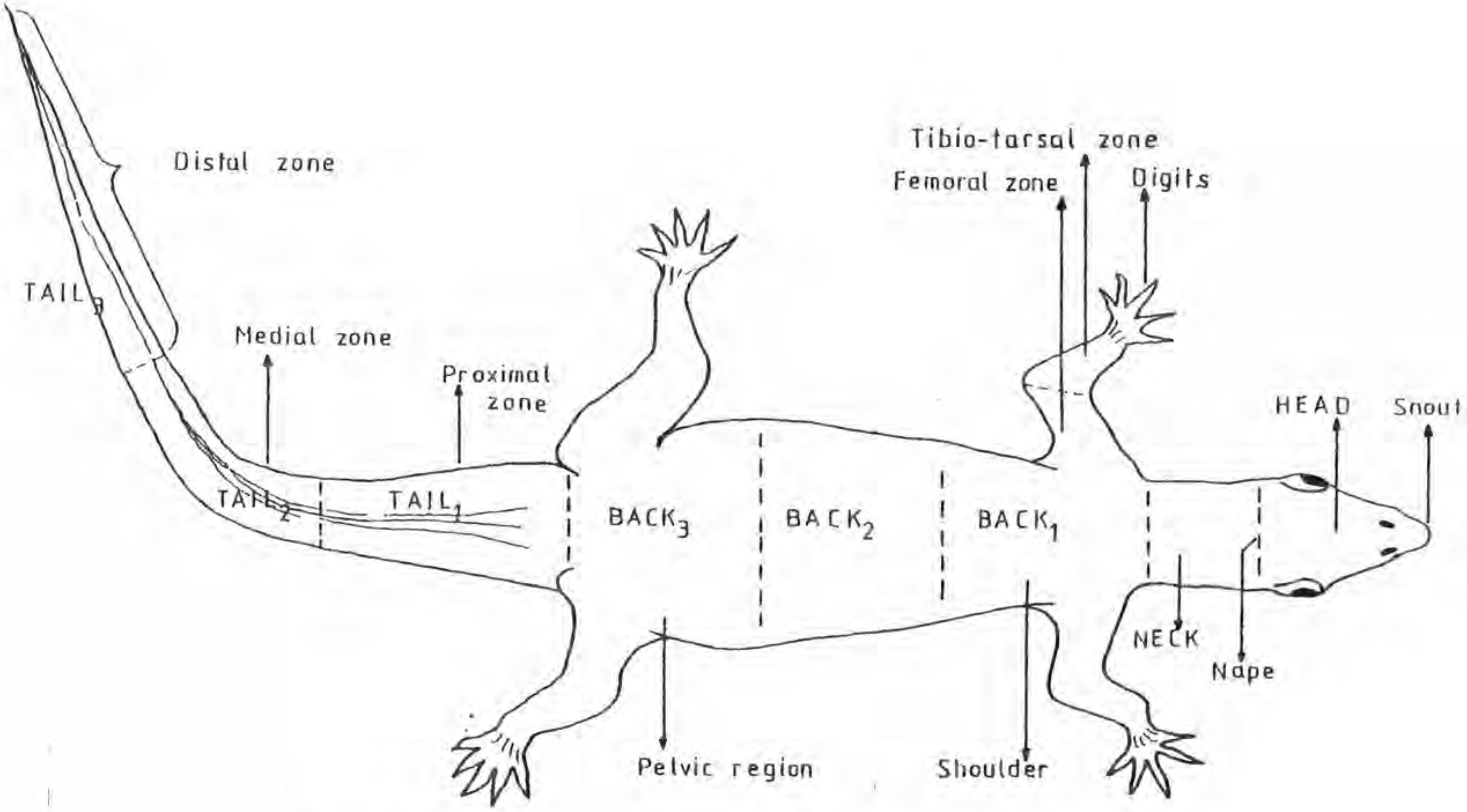


Plate 3: Sketch of a Nile monitor lizard, showing how body zones were mapped to describe the landing/biting-sites of *Glossina f. fuscipes.*

3.2.2 Body zone choices of *G.f.fuscipes* on the monitor lizard

One monitor lizard was placed at a time inside a wooden cage (92x35x35 cm) with a metal base and fine wire mesh on the sides (Plate 4). The sensors of a digital thermoanemometer and a light-quantum-meter (radiometer) were set, hanging upside down in the cage to measure respectively temperature and intensity of solar radiation in the cage. A stop-watch was held to monitor the duration of the different behaviours. Tsetse flies were caught in biconical and pyramidal traps and used immediately for experiments in the field.

Ten flies were introduced inside the cage using a sucking-tube. The body zones of the monitor were named according to Plate 3. Flies responding (landing, probing, feeding) were recorded. The main parameters measured were: time, light energy (solar radiation) and ambient temperature inside the cage, body zone, lizard size, behavioural sequences. Each session comprised of 15 minutes under bush shade and 15 minutes under direct sunlight . Subsessions were alternated in the sequence sun1-shade1-shade2-sun2,... Flies were released through the sliding-door at the top of the experimental box at the end of each session.

3.2.3 Nature of cues for body zone choices

3.2.3.1. Anatomical background of body zone preference

Skin samples of 2x2 cm were taken from different body zones of 10 dead monitor lizards. The shape and configuration of scales, the colour, the interscale distance, the thickness of the skin are observed under a dissecting (x20) microscope with a micrometer. The area of the scale was approximated using the geometric formula for the most similar geometric figure.

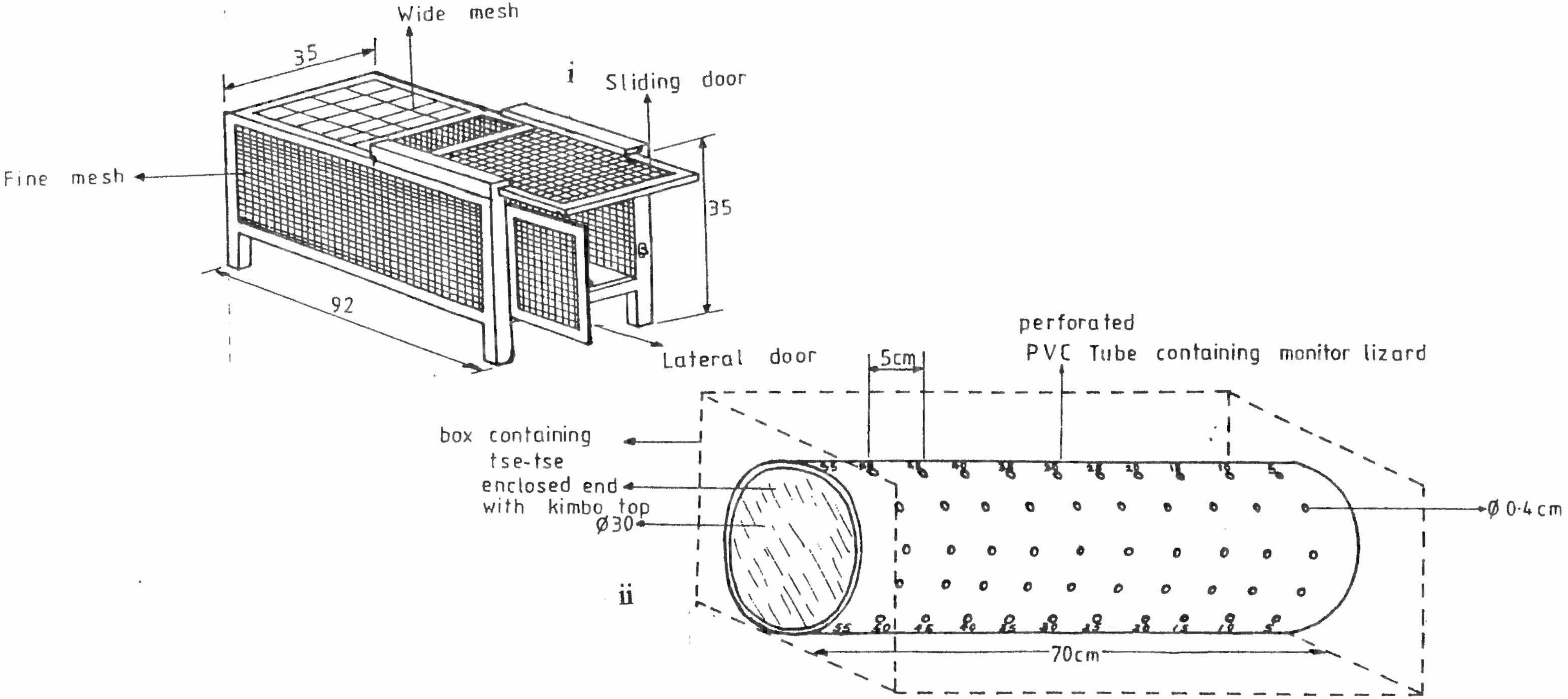
3.2.3.2 choices around a varan hidden in a perforated tube

There was first an attempt to know if flies could show some body zone preferences along the position of a varan which is hidden (visually). For that purpose, a monitor lizard was introduced inside a perforated PVC tube (15.5 cm dia.; length 74 cm), with holes of 0.5 cm dia (Plate 5) with rows of holes spaced 5 cm, and 3 cm within a row. The tube was put inside a wooden box surrounded with very fine mesh.

Thirty tsetse flies caught freshly in the field were released inside the cage and the experiment was conducted under direct sunlight for 30 minutes per session. An empty, clean similar tube was used as a control. The frequency of landing at 0-5-10-15-...70 cm from the side where the head of the lizard was positioned was measured.

3.2.3.3 Body zone choices on a dead defrozen varan used as a model for responses to shape and reflectance

The responses of *G. f. fuscipes* to shape and reflectance (without an interference of any kairomones) on the monitor were tested using specimens which were frozen since 3-24 months. The shiny appearance of the skin of specimens and colours were satisfactorily preserved in the deep-freezer. Sessions similar to the



Plates 4-5: Experimental device for the observation of (i) body zone choices of *Glossina f. fuscipes* and of (ii) landing positions on a perforated PVC tube in which a Nile monitor lizard was hidden.

experiment on body zone choices on a caged live varan were undertaken. Each session was 15 minutes under direct sunlight , between 1000-1400 h (local time).

3.2.3.4 Collection of odours from different body zones of the varan

To detect the presence or absence of the compounds from the varan which had been found active in GC-EAG assays (Prof. Hassanali, pers. comm.), hexane swabs were done on selected body zones. Clean pieces of cotton wool imbibed with hexane , held with forceps to avoid any contamination by fingers was rubbed each onto a distinct body zone (head, neck, shoulder, pelvic region of the back and proximal part of the tail.

Five varans were used in this process. Only pieces of cotton wool rubbed on the same body zone and held with the same forceps were kept together in a same container (100 ml). Each rubbing took 15 seconds. This duration was monitored using a stop-watch. Pieces of cotton wool rubbed on a specific body zone and put in the same vial containing hexane were shaken thoroughly and removed. The liquid was poured in distinctly labelled vials for each body zone of 50 ml. Each 50 ml sample was blown under a stream of nitrogen at 0 °C to 100 µl.

3.2.3.5 Gas chromatography

Gas chromatography analyses (GC) were carried out with the equipment HP 5890 II interfaced with the integrator HP3396 II. The capillary column was a methyl silicone ultra I (50m x 0.2mm x 0.32 µm), with temperature programming from 60 °C to 280 °C (10 minutes) at 5 °C/minute. Injector and detector temperatures were respectively 250 °C and 250 °C: Nitrogen was used as the carrier gas at a flow rate of 0.73 ml/minute. 2 µl of each concentrated sample were injected at each run.

3.2.4 Feeding behaviour on wild monitor lizards

Basking monitor lizards were observed using 10x50 binoculars from a bush hiding. Body zone, time, behavioural pattern were noted on a record-sheet. Scan sampling (where a group of lizards was rapidly scanned) was used in addition to focal sampling (where a given individual was thoroughly observed) during the same session. Continuous recording was used as long as a stable basking lizard was found, allowing observations for up to two hours.This was possible especially on tree trunks situated in littoral waters (Plate 6). Monitor lizards down on grass, on the shore tended to escape as soon as they noticed the observer.

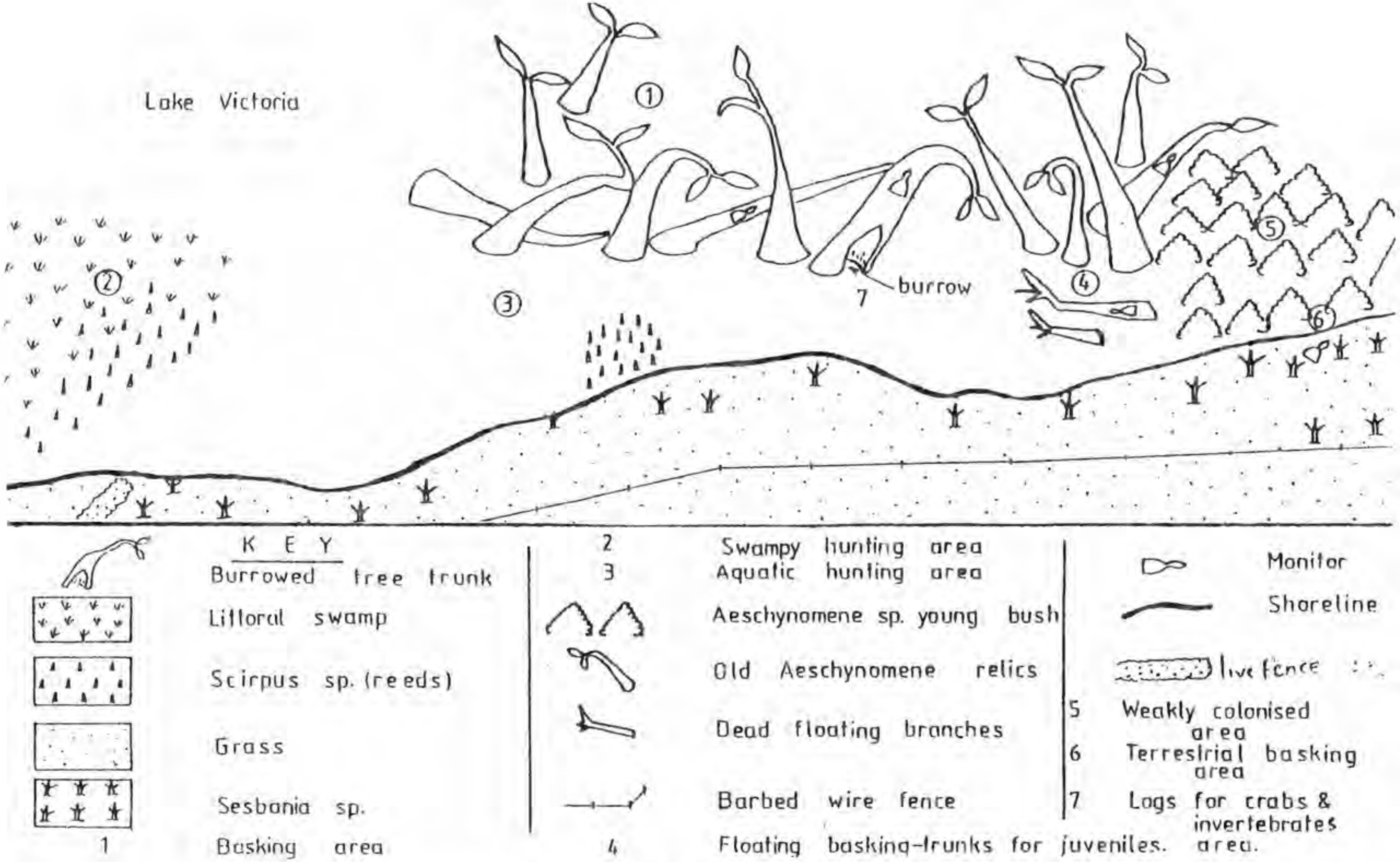


Plate 6: Diagram representing the site at Ogutu's farm (Mbita, Western Kenya) where the diel activity pattern of the Nile monitor was observed.

3.2.4.1 Co-occurrence of *G. f. fuscipes* and *V. niloticus* in nature

Biconical traps were set at 16 sites along the lakeshore. They were visited between 1130-1200 hours and between 1530-1600 hours (local time). At each visit, flies caught were sexed and counted, and varans seen at each site were counted. Means and variances of catches (males and females separately) and of lizard counts at each site were regressed to apply Taylor's power law on their distribution. Field binoculars were used to record numbers of tsetse feeding on varans. Each site (biotope type) was characterized using the following descriptors: (code in brackets):

i) whether the vegetation on the lake side is ontinuous (con) or discontinous (dis)

ii) whether the vegetation is bushy (den) or not dense

iii) whether the background or the side is open (open) or closed (clos) presence or absence of a corridor

Weather was also characterized as sunny or overcast, yielding the criteria: sunny morning, or overcast morning (at 0700-1200 h) sunny afternoon, overcast afternoon (1200-1600 h).

Mean counts of male flies, female flies were respectively regressed against the maximum (and mean) number of varans seen at each site. The relationship was considered as weak when $r < 0.50$, moderate when r varied between 0.50-0.80, and strong $r > 0.80$.

Counts of monitor lizards, male flies and female flies were classified by biotope types (descriptors i, ii, iii combined; i.e denconopen=site with dense vegetation, continuous on the lakeside and open or with a corridor), by weather and part of the day combined (i.e sunny morning). The classification was done using the canonical discrimination function (Digby and Kempton 1987) after log 10 transformation (candisc, SAS 1987).

3.2.4.2 Pattern of the diel activity of the varan

The pattern of the diel activity of the varan was studied at a site where 10-12 varans were observed every day on tree trunks in water inside the littoral zone. This site is represented on Plate 6. Ten visits were done early from 0600 h to monitor the hour of the first haul-out. Continuous sessions were organized to record the intraspecific interactions of the varans. Tsetse flies landing on the varans and the heights and angles for basking were also recorded like at several other sites. Basking heights and angles were estimated visually. These sessions helped to prepare the record-sheet for the hourly sessions on the basking behaviour.

Observations with 10x50 field binoculars were done hourly from 0800 h to 1800 h. Behavioural acts were written on a record-sheet. The behavioural repertoire included haul-out, basking, haul-in, hunting, swimming acts.

The relation weight-length of the varan was estimated. The total length was measured from the tip of the snout to the distal end of the tail of dead varans. Varans were weighed. The decimal logarithm of weights (kg) and of length (cm) was calculated. The relationship weight-length was obtained by de-linearizing the relation:

$$\log10\ (\text{weight}) = \log a + b \log\ (\text{length})$$

3.2.5 Anemotactic flight of *G. f. fuscipes* toward the Nile monitor

Male flies collected in the afternoon from the field (10 traps at scattered sites) were released with a suction tube into a wooden cage with fine wire mesh and 3 compartments joined (each to the next) by a central opening (Plate 7). The lizard (live = treatment or stuffed = control) was put in an adjacent cage with larger wire-mesh on the junction face. The experiment started at 1500 h and the number of flies in each compartment was counted at 1800 h. At such time the wind direction at the experimental site is from lake to land (West to East). The cage with the odour source was positioned westward). Phototaxis was reduced by working strictly under tree shade (Fig. 23). Flies in compartment (a) were non-responders; flies in compartment (b) started search and abandoned; flies in compartment (c) flew upwind but stopped in the close-range and flies in the odour compartment (d) alighted or attempted to alight (even feed). Details on this last component are detailed in the cage experiments on body zone choices. Total numbers were weighted by using only proportions of each total in the Anova.

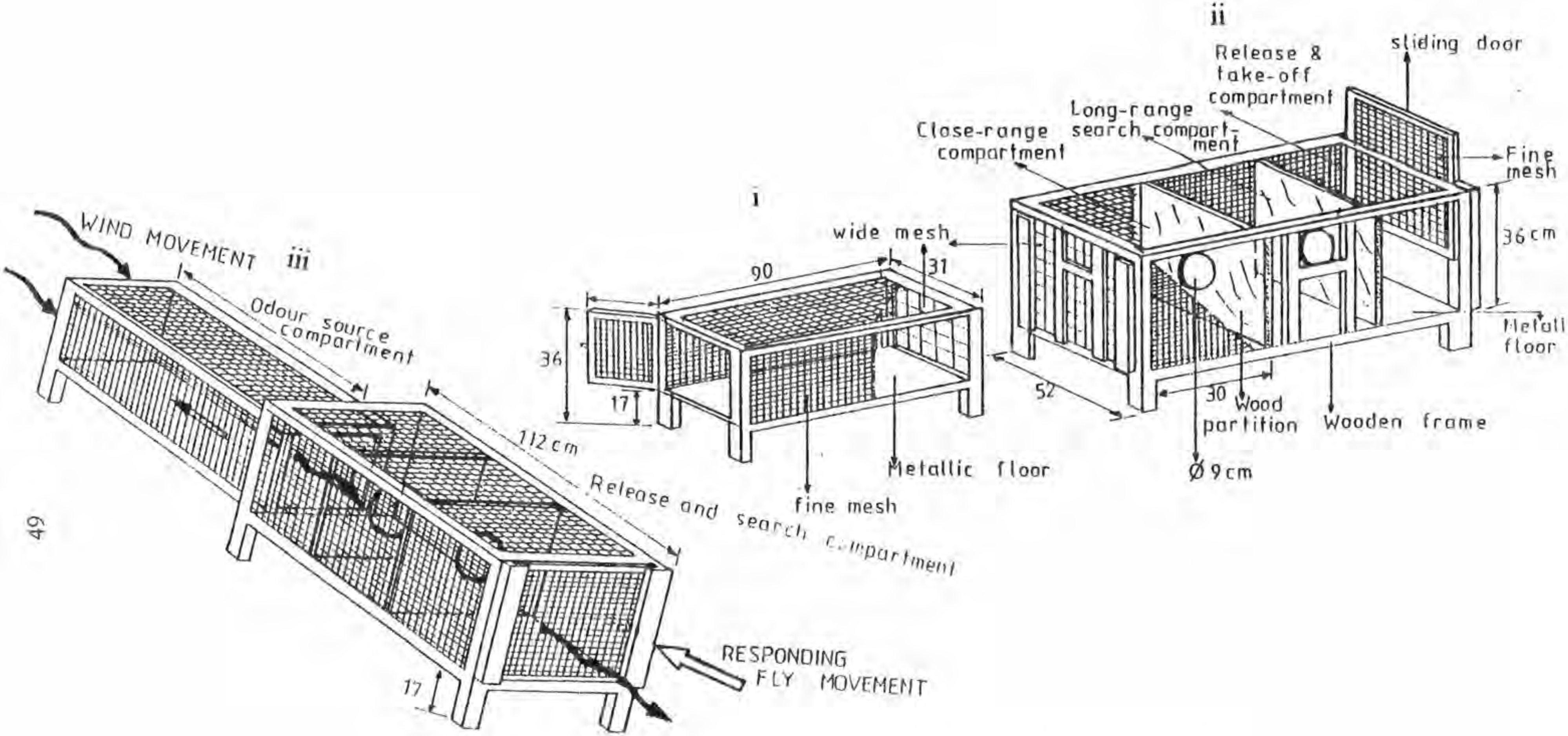


Plate 7: Sections of the wooden flight chamber designed to study patterns of upwind flight of *Glossina f. fuscipes* towards the Nile monitor: (i) odour compartment (ii) release, search and close-range compartments (iii) functional mechanism.

3.3 Trapping experiments

3.3.1 Attempts to improve the visual attractancy of traps

3.3.1.1 Validation of two-choice experiments

To check if a multiple choice situation can provide an unbiased information on colour and shape preference by *G. f. fuscipes*, I used a biconical and a pyramidal trap; their scores are already known as very similar from conventional latin square designs. There was no significant difference in the catches of both sexes, and of adults and tenerals from the standard biconical trap and the standard blue/black pyramidal trap. All categories had a catch index close to 1.0; except for female tenerals which had an index of 1.88 in favour of the pyramidal trap.

3.3.1.2 Comparison of standard traps with some candidates comprising of blue and red combinations

The purpose, here, was to select the best candidate trap in the blue/red combination. Three red colours different by their brightness were used (namely, Turkey Red 721/3, Peony Purple 729/1 and Doge Purple 732/1 according to the chart of the British colour Council (Wilson, 1938). The biconical and the pyramidal shape were tried (plate 9). Apart from the shape, the position of the red component was also tested as follows: i) red inside the biconical trap, no black, royal blue outside

ii) red alternating with royal blue outside, black inside the biconical trap

iii) red instead of black on the wings of the pyramidal trap.

To check if a bias was introduced when trapping assays for *G. f. fuscipes* were done in multiple choice, the standard biconical and pyramidal traps were set together at one site. They were spaced 2 m and visited every 24 h. The traps were shifted alternatively at each visit (11 replicates). Flies were killed by squeezing the thorax, sexed, classified as non-tenerals or tenerals and counted.

Comparisons against standard traps (i.e. pyramidal blue/red vs pyramidal blue/black and blue/red biconical vs blue/black biconical) traps were done in multiple choice tests. The treatment and the control traps were positioned every time at the same site at a distance of 2 m one from the other. Each experiment was replicated 5-7 times at any one site. It was repeated at three other sites different by vegetation, and fly abundance.

3.3.1 3. Comparison with the best candidate trap

The best candidate trap was tested against the standard blue/black biconical trap (Challier *et al.*, 1977). Traps (control and treatment) were set in pairs (Dransfield *et al.*, 1986); intertrap distance 50-100 m at intervals of 100-200 m along a linear sampling transect on the lakeshore (Plate 1). Five pairs of traps were used at 10 sites (5 replicates within each pair).

3.3.2 Experiments with baited traps

The blue/red trap baited with cow urine was tested against the blue/black standard trap. Traps were tested in pairs (Dransfield 1986), first at the sites represented on the map (Plate 1) and in a more bushy area (Kisui at 12 km from previous sites). The intertrap distance was 50-100 m at intervals of 100-200 m along a linear sampling transect on the lakeshore.

The blue-red biconical trap baited with fresh monitor lizard urine was tested against the standard biconical trap. Traps were again tested in pairs (4 pairs) alternated every 24 hours (sites on Plate 1). Fresh varan urine was dispensed in a piece of sponge, imbibed to saturation (Gouteux *et al.*, 1995) and enclosed inside the biconical trap (Owaga, 1984). Urine was added on the sponge at each sampling-occasion. This urine was collected in a 5-litre cylinder disposed below a hole under the box where the varans were kept. The urine was poured in 100 ml vials and closed, and kept in freezer to avoid fermentation.

The blue/black trap baited with cow urine was tested against the blue/black standard trap. Traps were tested in pairs too (Dransfield, 1986), first at the sites represented on the map (Plate 1) and again in a more bushy area (Kisui at 12 km from the previous sites). 5-6 replicates were made within each pair of traps.

The effect of age of cow urine was controlled. Zebu urine was obtained every time from the same farmer (15 cows owned). It was labelled by date, kept closed at ambient temperature on a table in the laboratory. Zebu urine of 0-7 weeks was tested (i.e 0-1, 1-2 weeks...) with 4-5 replicates each weekly interval of age. Cow urine was dispensed in 200 ml vials placed down at 20 cm from the trap pole (Owaga, 1984; Dransfield et al., 1986 and Mwangelwa *et al.*, 1990). Acetone was dispensed at a rate of 14.2-23.8 g/day; 5-6 replicates were made within each pair of traps.

3.3.3 Detection of some factors that effect the catch index

The catch index is defined here as the ratio "catch in treated trap/catch in the control trap". Data from trapping experiments were used in order to check the effect of vegetation on the catch index. Each sampling site was scored according to its vegetation : 1 = very bushy; 2 = bushy 3 = clear

The catch index (mean ± standard error) was computed and compared between vegetation types (t-test after comparison of variances or Kolmogorov-Smirnov when variances were heterogenous). To find out the relationship between catch index and abundance of flies, the catch index at each site (mean or value at each replicate) was regressed against the catch from the unbaited (standard) trap at that given site and replicate. Means of catches (control and treatment) were classified as well by effect, i.e attractancy when there had been an increase of the catch in the treated trap; repellency when the control trap catches more than the treated trap.

3.3.5. Mechanism of the density-dependence of the catch index

Data from field binocular sessions where the behavioural repertoire of *G. f. fuscipes* around conventional traps (Vavoua, pyramidal and biconical trap) were used to find the relation between the intensity of "entering" into the trap and the number of flies “seen on the trap” at each subsession. For this purpose, data from each session of two hours were grouped into subsessions of 10 minutes. The ratio (number entering / total observed) was calculated for each 10-minutes subsession and regressed against the total number observed during the same subsession.

Dead male flies (decoys) were attached at each face of three biconical traps using a needle and a black thread. The number of decoys was respectively 5-10-20 uniformly distributed just on top of each of the two openings on the lower cone. These three biconical traps were compared in pairs with the standard. Intertrap distance 50-100 m.The catch index was regressed against the number of decoys set or remaining on the trap at each daily visit.

A standard biconical trap (blue/black Challier-Laveissière 1977) was set in the field at the lakeshore. A monitor lizard (2,100 g) in a PVC tube was ventilated with a fan which was run with a car battery 12 V (Plate 8). The tube was hidden with grass, at an elevation of 40 cm at a distance of 1.5 m from the pole of the trap (horizontal line). Thus the gas was flown over the whole trap and also dispersed to the bush at a speed of .ca. 0.5 m/s. The experiment started at 0930 h. Sessions with fan on (YES) and fan off (NO) were alternated every 30 min. The catch of males and females was counted at the end of each session.

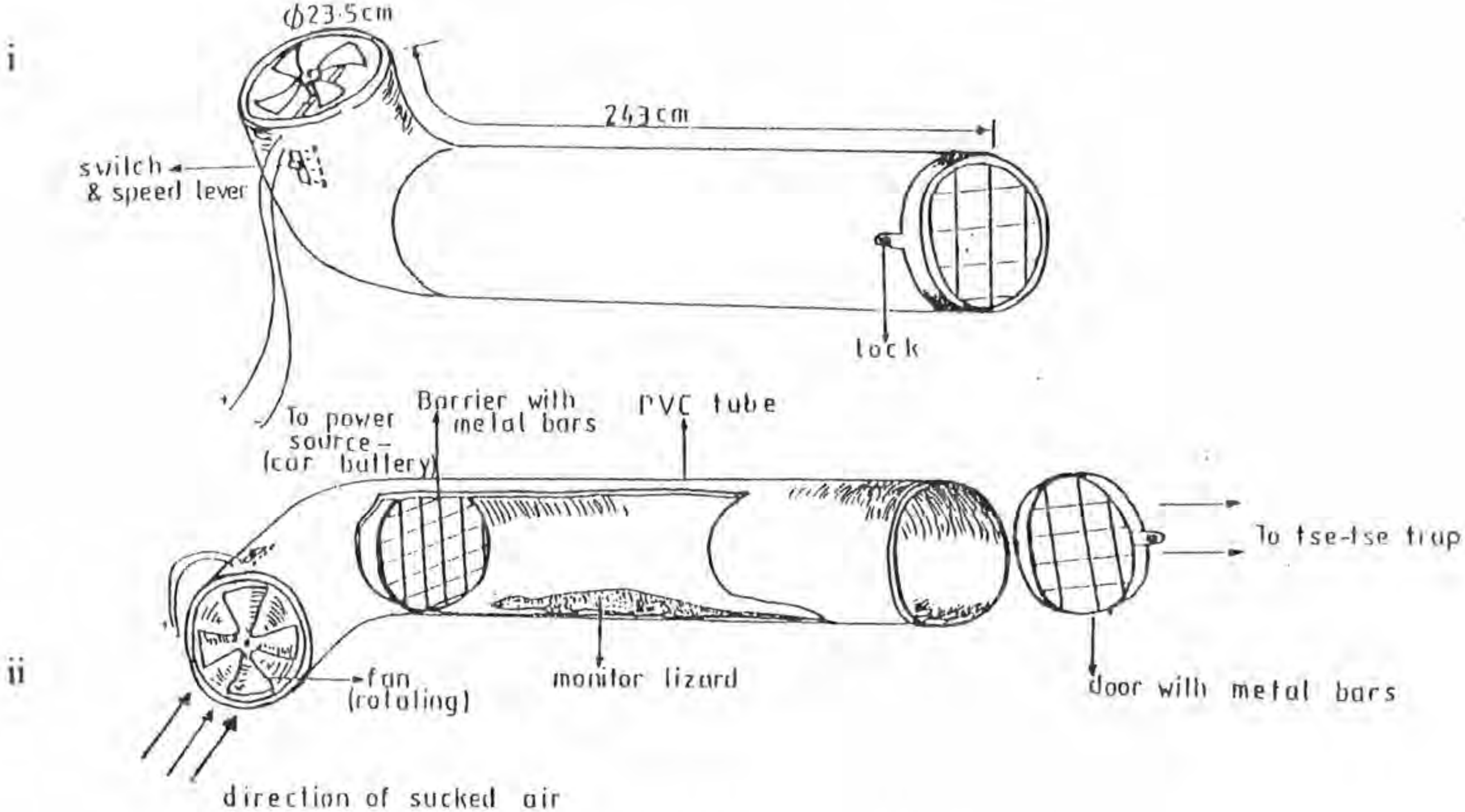


Plate 8: Experimental tube used to blow whole body odours of the Nile monitor in the field for baiting standard biconical traps: (i) general view (ii) longitudinal section.

1. 2 Electric screen

2. Blue/red pyramidal

3. Blue/red outside on biconical

4. Peony purple inside biconical

Plate 9: Some colour combinations used during this study: 1) on electric screens, 2) on a pyramidal trap, 3-4) on biconical traps. Pictures are not at uniform scale.

4. RESULTS

4.1 Colour and biotope preferences of *G. f. fuscipes*

4.1.1 Responses to single-coloured targets

Milling and landing responses of *G. f. fuscipes* to various single-coloured targets are shown in Table 2. Landing was similar on royal blue and on black. But, the milling around royal royal blue was not significantly different from that around blue/black, indicating an advantage of blue in this regards as compared to black (1.7x). Green and orange elicited only half of the score of blue/black for milling. Red stimulated significantly more landing than royal blue. This was shown both in an experiment with two choices and in an experiment with three choices. In a two-choice situation the intensity of the landing response on red (peony purple) cloth was more than double that of the landing on blue (P = 0.03).

Violet stimulated five times less landing than blue/black and three times less than red; and it attracted half of the level of blue/black; Yellow very consistently represented a minimum for landing. It attracted as much as violet (i.e. half of blue/black).

When single colours were separated by canonical discrimination according to their total catches, the following grouping occurred (Fig.4):

- yellow was a minimum, making a singleton
- orange and green were ranked together;
- blue, black and red offered the best performance.

Table 2: Responses of *G. f. fuscipes* to single-coloured cloth fabrics (set on electric screens) in Rusinga Island, Lake Victoria, Western Kenya. De-transformed means (% of the total catch of each experiment) are given.

exp no. (replicates)	treatment	Number of flies caught	landing (%)	spinning (%)	total (%)
1(6)	black	465	9.5b	12.2a	21.7b
	blue		11.1b	20.4a	31.5ab
	blue/black		21.5a	22.9a	44.4a
2(5)	green	296	2.6b	14.7b	17.3b
	orange		7.0b	16.9b	23.9b
	blue/black		20.2a	35.6a	55.8a
3(4)	Peoney purple	132	13.2b	17.4ab	30.6ab
	violet		7.9c	14.3b	22.2b
	blue/black		24.2a	22.7a	46.9a
4(3)	blue/white	161	3.5b	17.2a	20.7b
	yellow		1.9b	16.4a	18.3b
	blue/black		23.1a	37.8a	60.9a
5(4)	red	64	42.3a	19.8a	62.1a
	blue		17.3b	21.9a	39.2a

Ryan's Q test used for comparison after arcsine transformation. Different letters represent a significant difference between rows, within each experiment no.. where 3 targets are compared. Only experiment no. 5 involved 2 targets.

Blue and red were the only single colours which elicited a total approach not significantly different from that of the blue/black combination. Blue reached 90% and red 77% of the total catch of a blue/black target. In a 2-choice situation, red performed better than blue for landing (two-fold increase), yielding a 47% increase of the total catch as compared to blue (Fig. 3). Compared to a conventional single black target, blue yielded an increase in landing of 69% and red, 45%. However, none of the single colours could advantageously replace a blue/red or a blue/black target.

The selectivity of female or male flies to single colours was estimated as compared to the blue/black standard. On average, violet relatively attracted the same proportion of males and females as blue/black; so did blue. Green and red were relatively more selective to females than to males as compared to the blue/black standard. A very low proportion of males approached yellow; but a relatively higher proportion of males than females approached orange.

4.1.2. Responses to targets with combined colours

The blue/white combination elicited a very low landing response (6 times less than blue/black) and it was just equal to yellow for milling (Table 2). Blue/red performed slightly better than blue/black (Table 3) to stimulate the landing response (only 2% increase) but considerably better for milling (36% increase) (Fig. 3).When a blue/black/red combination was used on a target, no advantage was obtained in terms of landing (12% less than blue/black) and milling (7%) responses.

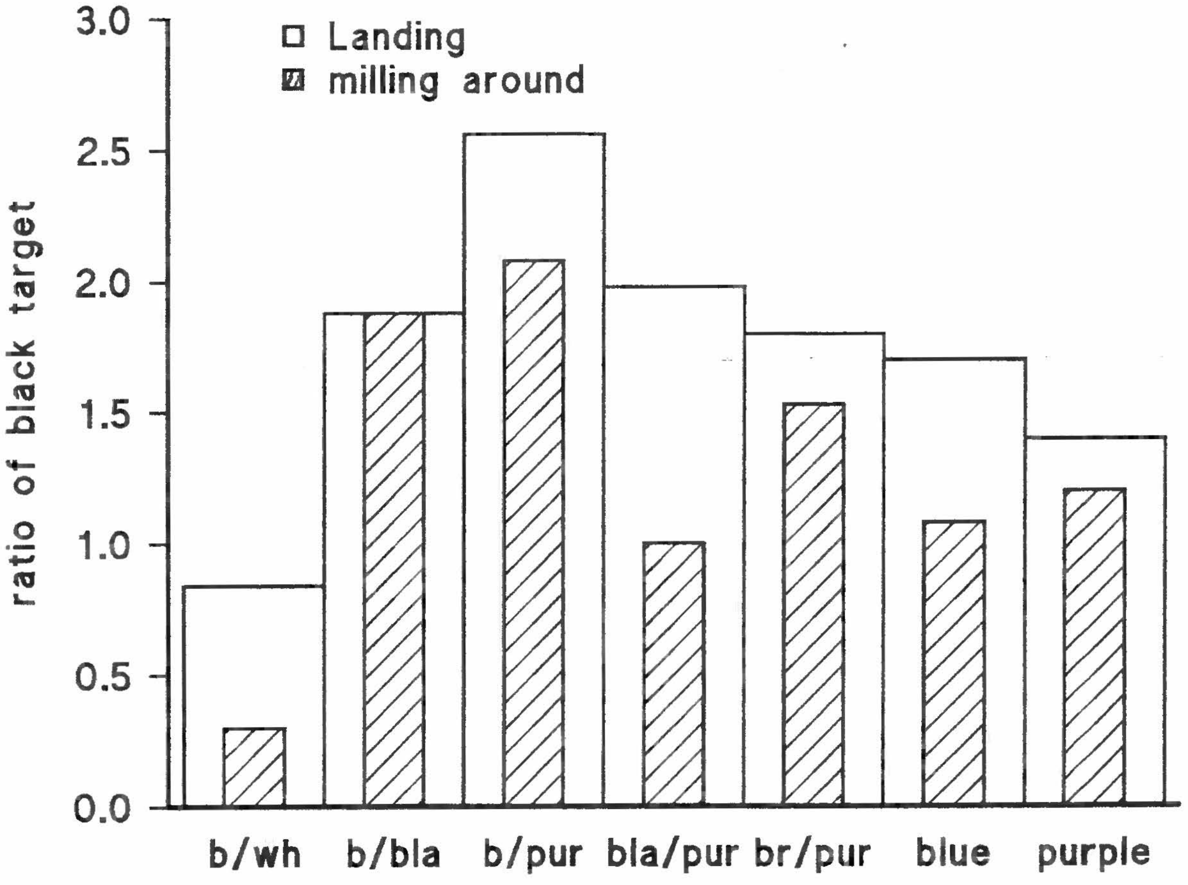


Figure 3: Best options proposed to replace the conventional black target for *Glossina f. fuscipes*. Performance of alternatives in terms of landing and milling around as compared to a black screen. b/wh = blue/white; b/bla = blue/black; b/pur = blue/purple; bla/pur = black/purple; br/pur= brown/purple.

Table 3: Responses of *G. f. fuscipes* to targets with combined colours of cloth fabrics (set on electric screens) in Rusinga Island, Lake Victoria, Western Kenya. De-transformed means (%) are given.

exp no (reps)	treatment	number of flies caught	landing	spinning	total
6(6)	blue/red	194	29.7a	20.0a	49.7a
	blue/black		29.1a	17.0a	46.1a
7(4)	blue/black/red	163	31.2a	19.1a	50.3a
	blue/black		27.7a	20.6a	48.3a
8(4)	red/black	82	18.4a	20.6a	39.0a
	blue/black		36.7a	18.7a	55.4a
9(5)	red/brown	106	25.9a	18.3a	44.2a
	blue/black		33.9a	18.7a	52.6a

Ryan's Q test used for comparison after arcsine transformation.

In the case of red/black, the landing response was only half of that elicited by a blue/black combination, though the milling behaviour was very close to that around blue/black cloth (4% increase). The performance of a red/brown target was very similar to that of a blue/black/red target. Combined colours significantly increased the landing response and the milling as compared to single colours, except a blue/white combination. For milling, a blue/red target was the best combination (2.6 times more milling than a conventional black target), followed by red/black (1.98) and blue/black (1.88 times) and red/brown (1.81 times). As far as landing is concerned, blue/red (2.08) and blue/black (1.88) were the best options (Fig. 3).

4.1.3 The wavelength basis of colour preferences

4.1.3.1 Effect of hue

The relationship between intensity of landing by *G. f. fuscipes* on a given cloth and its reflectance in the violet waveband was very weak; similarly, no relationship was found in the yellow, orange, red and infra-red wavebands (Table 4). The green spectral range showed a somewhat stronger relationship ($r^2 = 0.22$) but still non-significant ($P > 0.05$). On the other hand, an evident relationship was found between the intensity of landing and the reflectance in the blue waveband ($r^2 = 0.87$; $P < 0.01$). However, in this case, blue cloth itself was an outlier on the scatterplot, suggesting that an additional factor stimulates the landing-response on a blue cloth.

Table 4: Relationship between the intensity of landing and milling around by *G. f. fuscipes* under field conditions and the reflectance (%) of the experimental cloth fabrics within the different spectral wavebands from 390 nm to 1100 nm (regression coefficients r^2) ;* = signif. at P = 0.05; ** = signif. at P = 0.01.

independent variable x (waveband)	landing (r^2)	milling (r^2)
violet	0.002	0.17
blue	0.870**	0.30
green	0.22	0.01
yellow	0.007	0.10
orange	0.108	0.06
red	0.001	0.11
infrared	0.084	0.84*

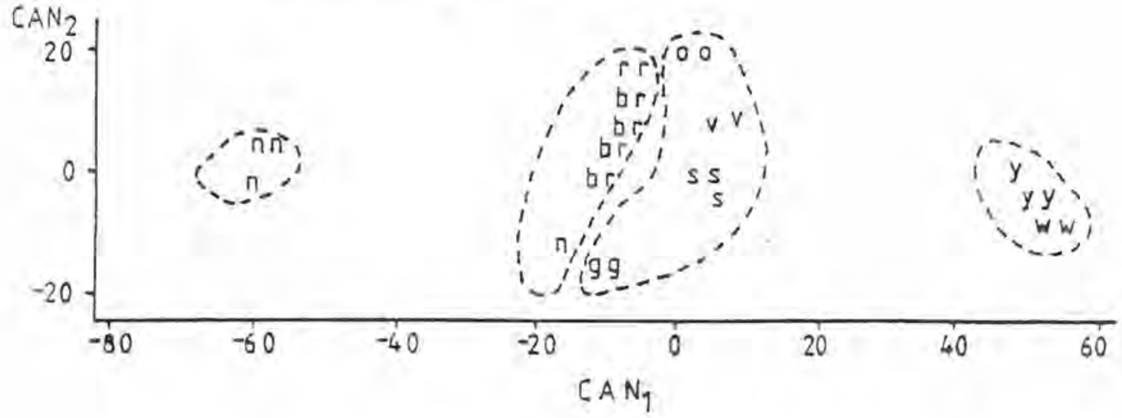
Taking account of the very strong relationship ($r^2 = 0.87$; P=0.008) between the intensity of landing of *G. f. fuscipes* and the reflectance in the blue waveband (450-490 nm), an attempt was made to predict the intensity of landing as a function of blue reflectance of the experimental materials. A satisfactory prediction was obtained for green, yellow, black especially and at a lesser extent for red and violet cloths (Table 5). Blue cloth was as an outlier. The value predicted for lizard skin (intensity of landing compared to a blue/black standard target) was moderate (25%) and comparable to that of violet cloth (23.6%), although higher than the one predicted and observed on green (11.1 %) and yellow (6.5 %) cloths; Infra-red reflectance of the experimental cloths was also used to predict the potential of the same cloths for milling ($r^2 = 0.92$; P<0.01). A very satisfactory relationship was obtained for blue cloth, violet, yellow, and orange cloths. The prediction was moderately successful for the red cloth; here, green and black stood aside as outliers, suggesting mediation of other factors in their milling. A very strong milling response was predicted for monitor lizard skin (95.8% as compared to a blue/black target).

Table 5: Attractiveness of the experimental material as observed (% of blue/black standard) and as predicted by the blue waveband hue for landing and by the infra-red reflectance for milling. Outliers are not included.

cloth	Landing %		Milling around %	
	predicted	observed	predicted	observed
violet	23.6	18.3	54.8	48.0
blue	-	53.0	93.7	90.9
green	11.1	12.7	-	42.7
yellow	6.5	8.3	46.8	45.0
orange	49.0	40.7	47.4	47.7
red	46.1	59.1	63.4	77.7
black	49.8	49.3	-	53.0
Lizard skin	25.9	-	95.8	-

i CLASSIFICATION BY REFLECTANCE

Plot of CAN2 * CAN1



ii CLASSIFICATION BY FLY CATCHES

Plot of CAN2 * CAN1

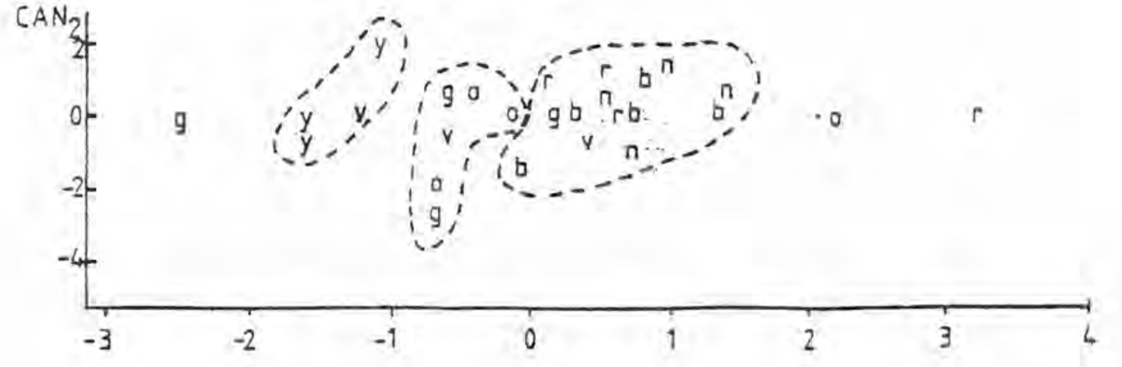


Figure 4: Classification (canonical discrimination) of experimental cloth fabrics by (i) their reflectance (%) values and (ii) their catches of flies on electric screens in the field. n = black; b = blue; r = red; o = orange; v = violet; s = lizard skin; g = green; y = yellow; w = white.

In the absence of an opportunity to run electroretinographic and phototactic experiments here, the visual sensitivity of *G. f. fuscipes* was tentatively assessed. I used the same regression coefficients between the milling around behaviour or the intensity of the landing response of *G. f. fuscipes* under field conditions and the reflectance within the colour spectral ranges (Table 4).

The coefficients suggested a moderate sensitivity to near ultraviolet, violet ranges (390-450 nm). A shoulder appeared in the blue waveband (450-490 nm); with a very steep decrease in the green region (490-560 nm); a weak sensitivity was suggested in the yellow (560-590 nm) to orange waveband (590-630 nm), increasing somewhat in the red waveband (630-760 nm). A very strong sensitivity is suggested in the near infrared (760-1100 nm).

The pattern of landing was almost an accurate replication of the classical model of sensitivity of *Glossina* where a very clear peak occurs in the blue waveband and a moderate shoulder in the orange waveband, with a minimum in the yellow region of the spectrum. However, the performance in the invisible region (ultraviolet and infra-red) was different in this case.

In conclusion, blue, red and black cloths have the strongest potential to attract *G. f. fuscipes*. It is tentatively suggested that *G. f. fuscipes* has a good perception above the upper side of the visible waveband; and a very moderate use of the near ultra-violet, while keeping the classical pattern of *Glossina* in the blue waveband.

4.1.3.2 Effect of chroma

The classification of experimental cloths by their reflectance intensity (cluster analysis) yielded two groups: very bright colours (white and yellow) and duller colours (black, blue, green, lizard skin, red, violet, brown and orange) (Fig. 4).The bright colours (Fig. 5; Table 6) showed poor performance both for milling and landing of *G. f. fuscipes* (Table 2). Among red cloths, the best candidate had a lower reflectance in the infra-red range despite similarities from violet to orange wavebands (Fig. 6). Earlier, it was shown that blue and infra-red reflectance accounts well for the poor performance of yellow. White cloth strongly reduced the attractiveness (caused repellency) of royal blue, bringing the performance of the blue/white combination to a minimum (or to the same level as the yellow colour). This would question the use of the bright U-V-reflecting white net which is used on the upper cone of the conventional traps. All the colours with high performance were duller (red, blue, black). Infra-red reflectance accounted very satisfactorily for the strong attraction towards blue and red (infrared reflectance); but the efficiency of black cloth might depend on its overall dull look, emphasizing the importance of silhouette as another factor for medium range perception. Such a factor may also play a role when the lizard assumes a darker colour while basking.

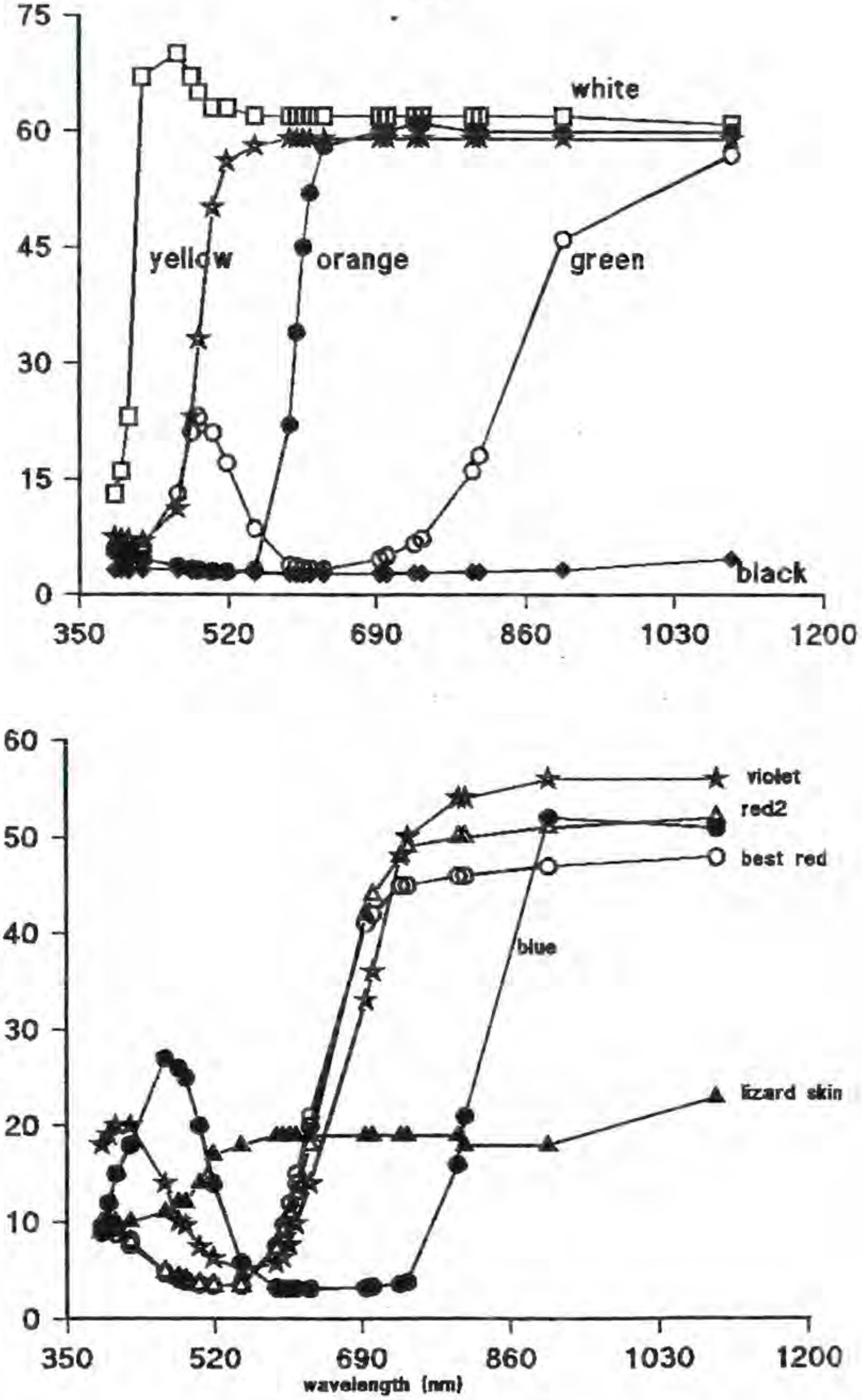


Figure 5: Reflectance of the experimental cloth fabrics and of the Nile monitor skin.

Barium sulfate was used as standard sample.

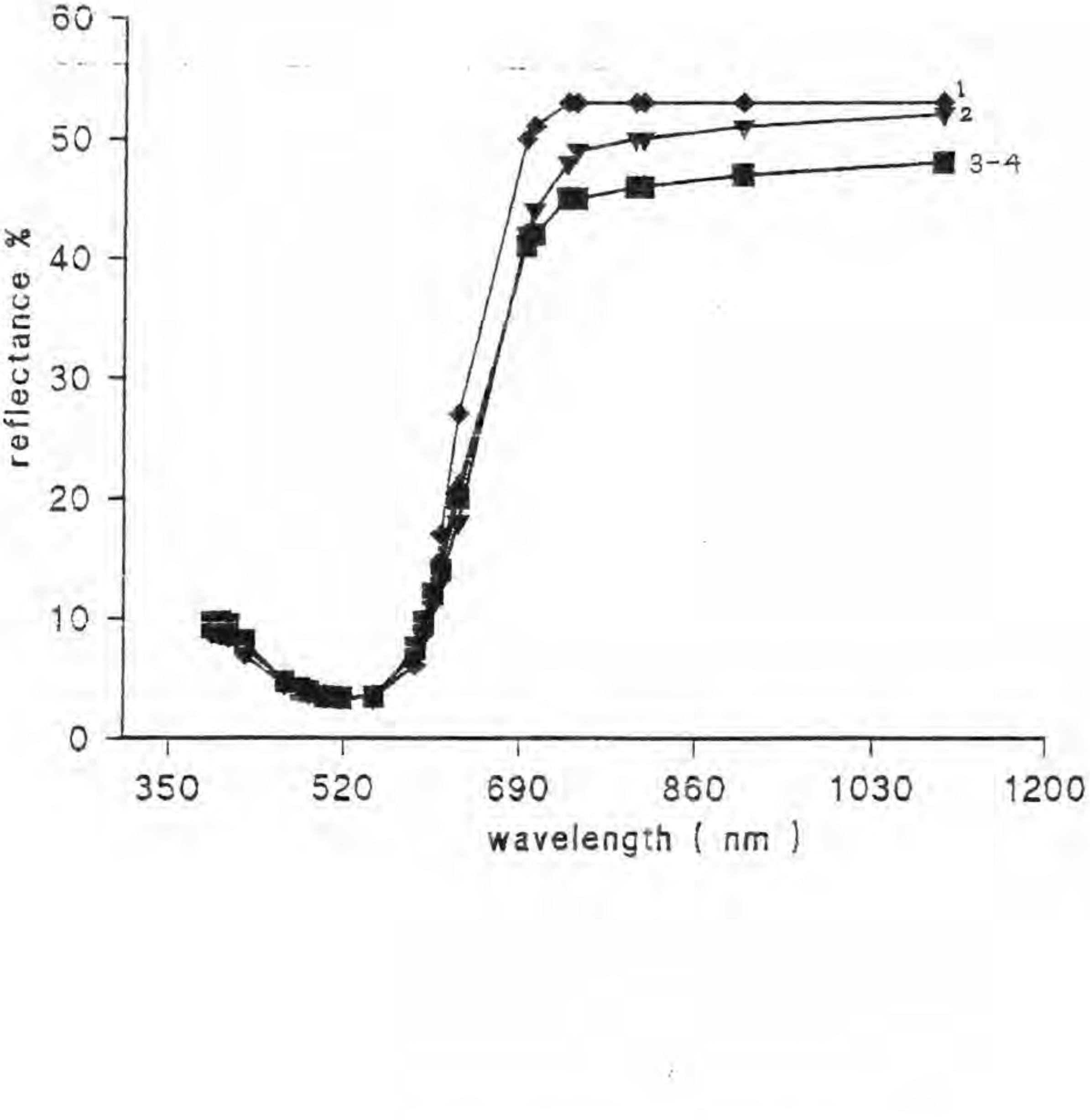


Figure 6: Reflectance of the red experimental cloth fabrics, stressing their differences in colour intensities. 1 = Turkey red; 2 = Doge purple; 3-4 = Peony purple.

Since the landing behaviour on the royal blue cloth could not be accounted for by reflectance, this cloth might simulate a shadowy appearance to the insect.

4.1.3.3 Quantum reflectance as another predictor of the attactiveness of colours

The relationship between quantum reflectance and landing showed that black, orange, brown, the 3 reds, and monitor lizard skin could be strong stimuli. Violet, green, yellow, white were predicted to be weak stimuli. Blue cloth was an outlier on the scatterplot, indicating that a factor other than reflectance explains its stimulation of the landing (Table 7). The same was true for milling around green. The relationship showed that black, monitor skins, and royal blue are very strong stimuli for milling ; turquoise blue, red and brown cloths were moderate stimuli. White, yellow and orange were potentially weak attractants. This general pattern is close to our observations (Fig. 7).

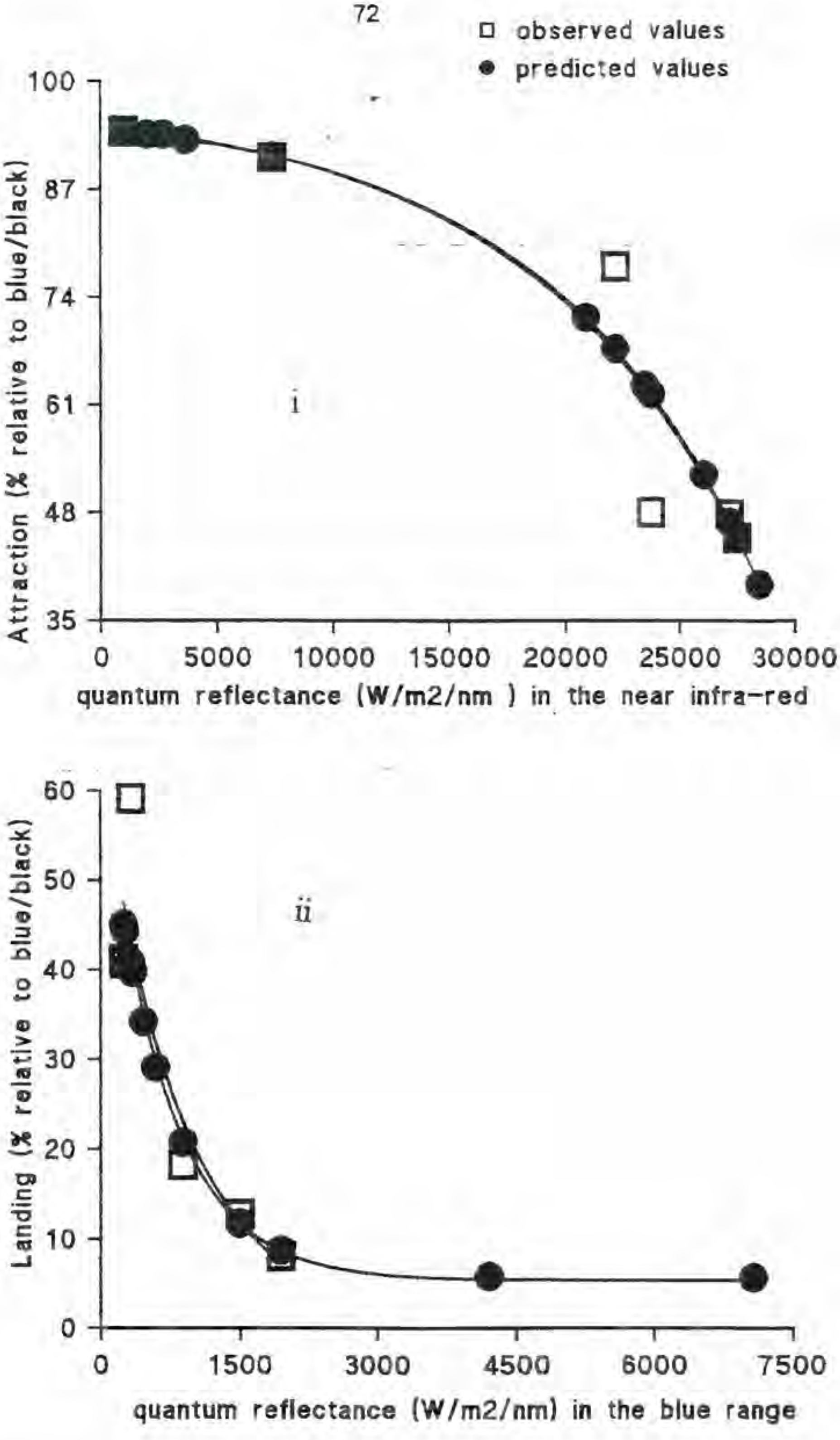


Figure 7: Relationship between (i) the orientation potential (ratio of a blue/black target) of colour fabrics for *G. f. fuscipes* and their quantum reflectance in near infra-red: $Y = 97.08 - 2.74 \exp(0.000107 X)$; $r^2 = 0.82$; $P < 0.05$).

and (ii) the potential to elicit a landing response and the quantum reflectance in the blue range: $Y = 5.71 + 57.13 \exp(-0.0015X)$; $r^2 = 0.98$; $P < 0.01$.

Table 6: Reflectance (%) values of experimental materials. A piece of monitor lizard skin was also scanned.

cloth	Wavebands						
	violet	blue	green	yellow	orange	red	infrared
violet	19.0	12.3	6.2	5.4	9.9	35.2	53.6
blue	17.5	26.4	12.4	3.6	3.1	3.3	20.1
green	6.1	16.7	14.6	4.7	3.3	4.0	17.9
yellow	7.0	18.3	54.4	58.5	59.0	59.0	59.0
orange	4.7	3.4	3.0	11.3	49.0	60.3	60.0
red	7.7	4.4	3.4	5.4	15.1	35.0	46.2
black	3.2	3.1	2.8	2.7	2.6	2.6	2.8
brown	6.0	4.0	4.4	6.0	6.8	16.9	59.0
white	48.8	68.6	62.5	62.0	62.0	62.0	62.0
skin	10.3	11.5	17.0	19.0	19.0	18.3	18.2

Table 7: Mean Quantum reflectance values (W/m^2/nm) of the experimental colours. The landing is predicted by the irradiance in the blue waveband ($r^2 = 0.98$; $P < 0.01$) and milling is predicted by the irradiance in the infra-red waveband ($r^2 = 0.82$; $P < 0.05$). Gaps indicate outliers.

Colour	mean within 450-490 nm	mean within 760-850 nm	predicted landing % relative to blue/black	predicted milling % relative to blue/ black
1. Amethyst violet	888	23733	20.7	62.3
2. Princes blue 745/3	2267	7366	-	91.0
3. Faience Blue 649	4205	20844	-	71.6
4. Jade Green 54	1497	6102	11.7	-
5. Sulphur Yellow 1/1	1945	27511	8.7	45.0
	261	27177	44.3	46.9
7. Turkey Red 721/3	322	26044	40.9	52.6
8. Peony Purple 729/1	330	22144	40.5	67.8
9. Doge Purple 732/1	337	23444	40.2	63.4
10. White	7087	28488	5.7	39.3
11. Grayish Brown	317	25800	41.2	53.8
12. Black	247	982	45.1	94.0
13.monitor neck skin	595	3650	29.1	93.0
14.monitor back skin	346	2003	39.7	93.7
15.monitor leg skin	463	2718	34.2	93.4

4.1.4 Light preferences of *G. f. fuscipes*

The curve of solar illumination (radiometric measurements in µE/m²/S) at Rusinga is bell-shaped as expected. The sunrise usually occurs at ca. 06:30 (Kenya Meteorological Service in KBC) in this Western part of the country. In the interval 0630-0800 h, light energy is low. (50-200 µE/m²/s) (Fig. 1). At 0900 h it can reach ca. 900 µE/m²/s, and at 1100 h it can reach as much as 1500 µE/m²/s. Usually from 1100-1400 h, light radiation is above 1,500 µE/m²/s, frequently reaching 2,100 µE/m²/s which characterize a very bright day in international standards (Li-Cor manual, 1991). The decrease in light energy starts at ca. 1500 h, to reach ca. 800 µE/m²/s at 1700 h, and ca. 300 at 1800 h and almost 1 µE/m²/s at 1900 h.

An estimate of the frequency of overcast days (solar radiation maximum less than 500 µE/m²/s) and bright days (light radiation between 500-2000 µE/m²/s) shows that at most ca. 20% days of a month are overcast (Fig. 1). This is particularly true in February, June, July, August, September. The frequency of dull days could reach 30 % in April during the heavy rains. Usually, 7-8 hours of sunshine are observed in this area. Only the rainy months of April and November can go as low as 6 hours on average (heliograph data, cv 43-47%).

4.1.4.1 Solar illumination and the attractiveness of conventional traps

The approach response to biconical, pyramidal and Vavoua traps was recorded using field binoculars at hours of peak activity of *G. f. fuscipes* (1100-1400 h). A clear maximum was observed on the biconical trap in the region 1,600-1,700 µE/m²/s (Fig. 8). A gradual decrease occurred above 1,700 µE/m²/s in the region 1,700-2,000 µE/m²/s. This suggests that the light preferences for the fly is in the region 1,600-1,700

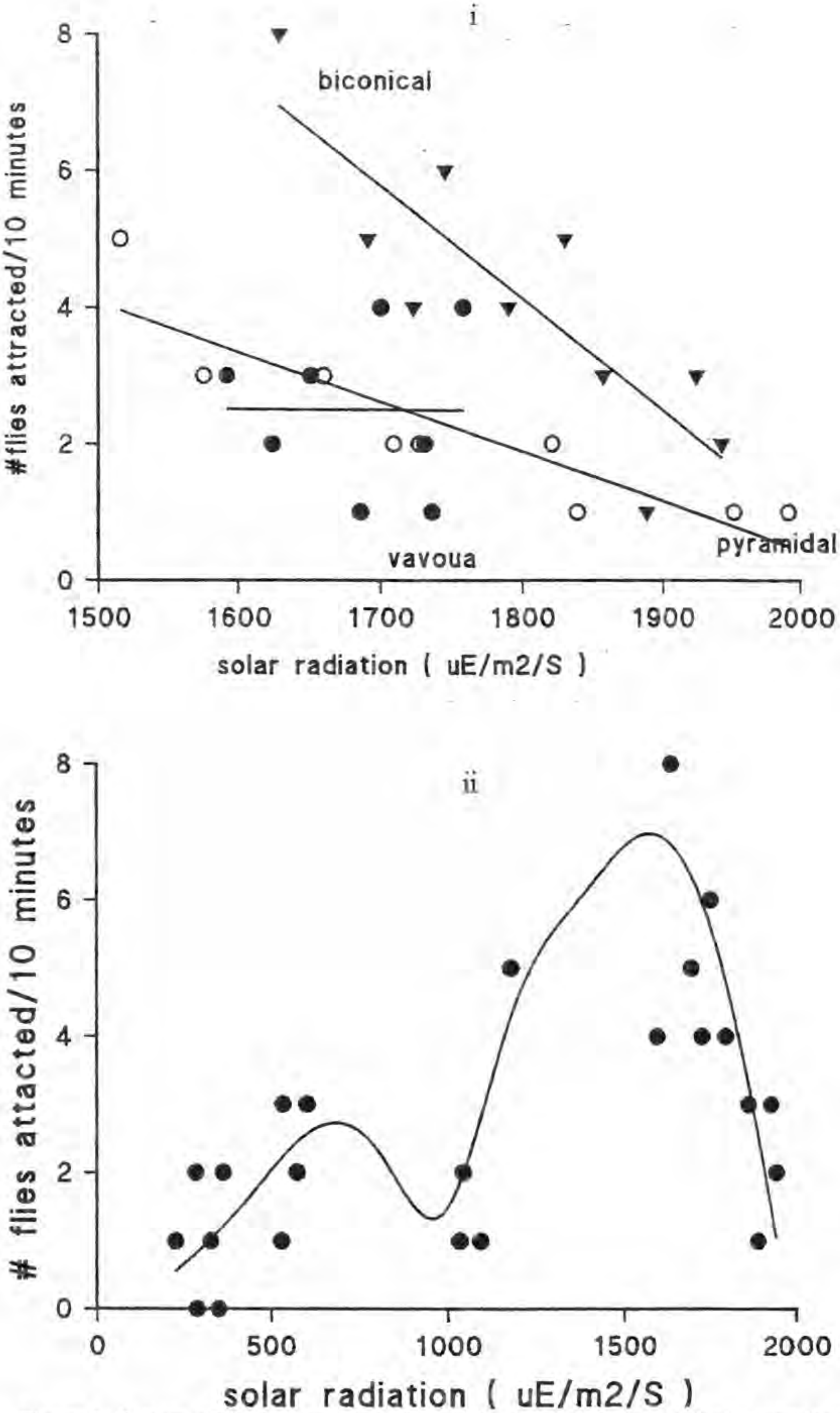


Figure 8: Pattern of (i) the attraction of *G. f. fuscipes* towards biconical, pyramidal and Vavoua traps within the ranges of solar illumination which characterize the time of peak activity; (ii) the bimodal shape of the approach of *G. f. fuscipes* to the standard biconical trap under various solar illumination levels.

μE/m^2/s and that the response of the fly becomes photonegative when the radiation is too high (above 1700 μE/m^2/s).

On a Vavoua trap, the intensity of the approach response decreases from 1,500 onwards, showing an evident photonegative response in the region 1,500-2,000 μE/m^2/s. The pattern on the pyramidal trap is similar to that on the biconical trap, but the amplitude of the response is clearly higher on the biconical trap. The means (± standard errors) of flies attracted during subsessions of 10 min. were respectively: 4.09 ± 1.92 for the biconical ; 2.5 ± 1.30 for the pyramidal and 2.0 ± 1.40 for the Vavoua (n = 9-10).

4.1.4.2 Biotope preference as a consequence of light preferences

A number of factors was investigated in relation with biotope and light preferences: areas of corridors (open space within vegetation), time of day (morning or afternoon), the status of vegetation cover (dense bush or not, and continous vegetation on lakeshore side or not) and light regimes (bright >500 μ/m^2/s or overcast <500 μ/m^2/s). The relationship between the areas of corridors where traps were placed and the catch of females was weak ($r = 0.47$; $P < 0.1$). The relation between the same and the catch of males was very weak ($r = 0.19$). Canonical discrimination analysis (total df = 282) showed that:

- females were abundant by sunny morning and sunny afternoon (Table 8).
- males were slightly more abundant by sunny afternoon; but a factor other than weather and time of the day accounted better for the occurrence of males; that factor is vegetation.

Table 8: Coefficients and class means in the canonical discriminant analysis of male *G. f. fuscipes*, female *G. f. fuscipes* and monitor lizard classified by time and weather (total df = 282; within classes df = 279; between classes df = 3; cumulative proportion of eigenvalues can1 and can2 = 0.982).

Variables	Raw canonical coefficients		
	can1	can2	can3
males	0.885	-3.447	1.264
females	2.524	2.190	-1.066
lizards	-0.729	1.666	4.660
time and weather	class means on canonical variables		
dull morning	-0.563	0.027	0.048
sunny morning	0.170	0.340	-0.037
dull afternoon	-0.235	-0.364	-0.130
sunny afternoon	0.379	-0.178	0.040

- males appear to have a preference for bushy sites. Such sites can have a continuous vegetation or a corridor (open or closed) (Table 9).

- female flies were associated with continuous linear lakeshore vegetation with open background or corridor whether very bushy or with average thickets. Another factor explains better the occurrence of females than does vegetation types. That factor is sunlight (sunny day, morning or afternoon). Results showed that while the occurrence of males was determined by the presence of bushes , that of females was very dependent on light radiation (and not so much on the vegetation type). The requirement of a corridor in the biotope choice of females is again compatible with this need of high illumination.

It is suggested that the lower peak (ca. 400 $\mu E/m^2/s$) observed on the biconical trap could characterize males , because their light threshold is lower; and that the upper peak (ca. 1,600 $\mu E/m^2/s$) is a maximum of female activity. However, it does not mean that males are not found in the upper region; while females are expected to be very rare in the region < 500 $\mu E/ m^2/s$, males are still active in the upper region.

4.1.4.3 Light, temperature and sex-ratio

Fig. 9 represents the variation of the sex-ratio (F:M) under changing sunlight radiation. In the region 200-500 $\mu E/m^2/s$, males predominated. Practically no females were caught in the biconical trap under such low illumination. In the region 500-1,000 $\mu E/m^2/s$, females are already available, with ratios as high as 2.0-4.0. Such values are typical in traps at hours of peak activity of *G. f. fuscipes* on Rusinga Island.

There was a significant difference between sex-ratios in relative humidity ranges 80-85% rh and 85-90% rh (Kruskal-Wallis, $P = 0.04$). Thus, to a large extent, the activity

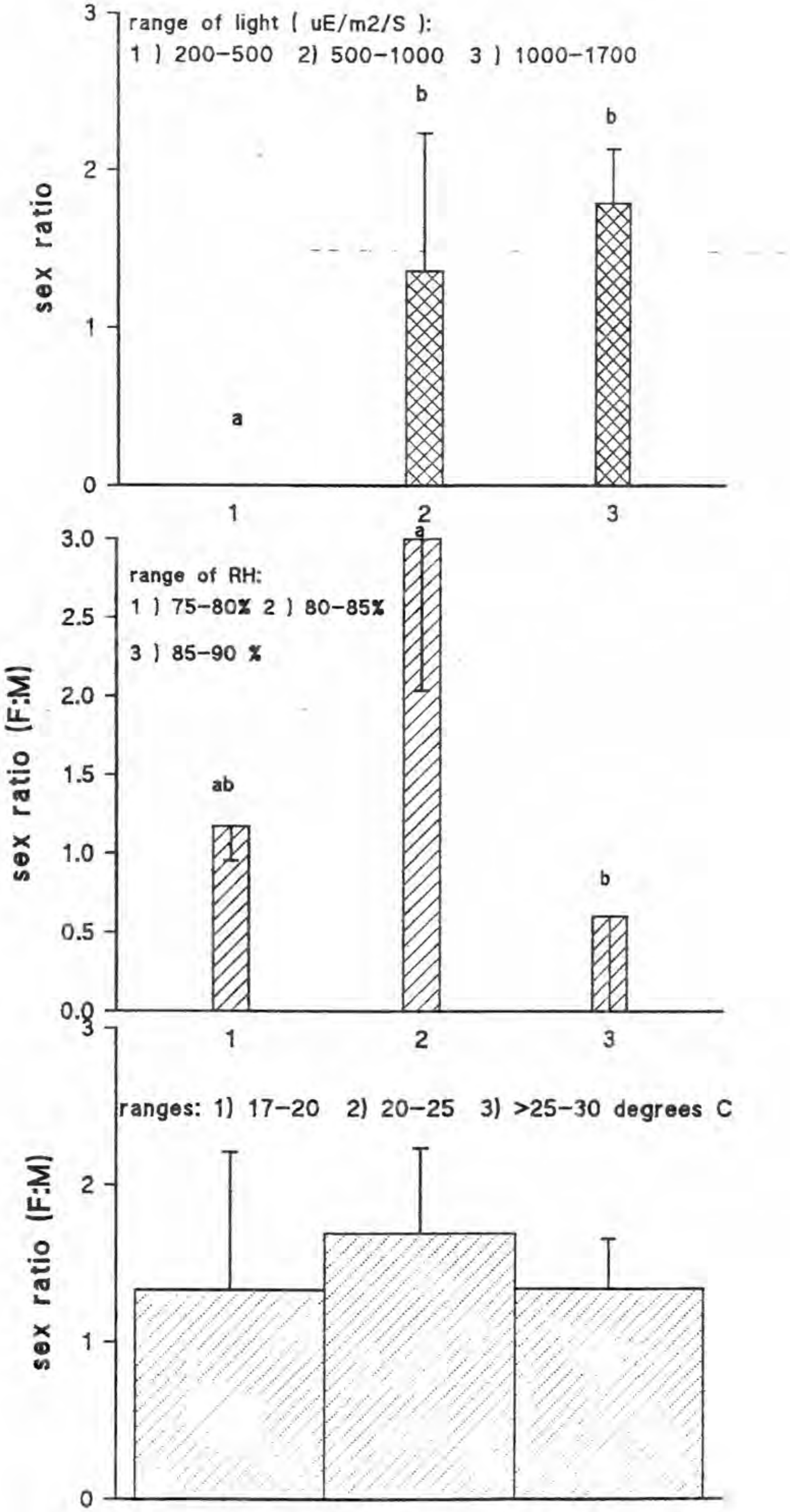


Figure 9: Variation of the sex-ratio of *G. f. fuscipes* within various ranges of (i) solar illumination (ii) relative humidity and (iii) ambient temperature.

Table 9: Coefficients and class means in the canonical discriminant analysis of male *G. f. fuscipes*, female *G. f. fuscipes* and monitor lizard classified by vegetation type (total df = 282; within classes df = 279; between classes df = 5; cumulative proportion of eigenvalues can1 and can2 = 0.995)

Variables	raw canonical coefficients		
	can1	can2	can3
males	0.885	-3.447	1.264
females	2.524	2.190	-1.066
lizards	-0.729	1.666	4.660
vegetation category	class means on canonical variables		
dense continuous not open	-0.650	0.508	-0.030
dense continuous open	0.460	-0.022	0.017
dense discontinuous not open	-0.557	-0.577	0.040
dense discontinuous open	-0.257	0.386	0.061
dense not on lake not open	-1.085	-0.329	-0.066
not dense continuous open	0.460	-0.060	-0.059

of *G. f. fuscipes* appears to be dependent on light radiation and on relative humidity and not on temperature.

4.1.4.4 Behavioural repertoire around conventional traps (biconical, pyramidal, Vavoua) and why the biconical trap performs better

The behavioural repertoire around the biconical trap was much richer than that on the pyramidal trap and the Vavoua (Table 10). On the biconical trap, as many as 14 elements of behaviour were observed; while on the pyramidal trap and the Vavoua, *G. f. fuscipes* just:

- alights and enters
- alights, performs short flights and takes off
- alights and takes off (Vavoua only)
- Performs short flights and enters (pyramidal only)
- alights, walks and enters (Vavoua only)
- enters directly
- alights, performs short flights, takes off (pyramidal only).

Very few acts took place on the upper cone (white netting) in the pyramidal trap and the Vavoua.

Table 10: Detailed behaviour of *G. f. fuscipes* around its conventional blue/black traps

no. Behaviour	% frequency occurrence		
	biconical	pyramidal	Vavoua
I. alight-enter	37.9	15.6	13.6
II. alight-fly-enter	5.2	-	-
III. alight-fly-take-off	5.2	-	4.5
IV. alight-fly-walk-enter	1.7	-	-
V. alight white-lowcone-enter	1.7	-	-
VI. alight white-lowcone-take-off	3.4	-	-
VII. alight-take-off	22.4	-	9.1
VIII. alight ring-enter	1.7	-	-
IX. alight white-lowcone-short flights-takeoff	1.7	-	-
X. alight-short flights-enter -	-	3.1	-
XI. alight-walk-enter	1.7	-	4.5
XII. enter directly	12.1	*56.2*	59.1
XIII. hover and go away	1.7	3.1	9.1
XIV. alight, short flights take-off	-	3.1	-

Table 11: Duration of the most frequent behavioural acts when *G. f. fuscipes* approaches the blue/black biconical trap

no.	action	trap zone	n	duration (sec.)
VII.	alight-take off	blue intercone	7	27 ± 8
		blue cone	5	124 ± 104
XII.	enter directly	openings	7	2 ± 0
I.	alight-enter	blue cone	20	38 ± 8
X.	alight-short flights-enter	blue cone	2	10 ± 2
XIV.	alight-short flights-takeoff	blue cone	2	170 ± 130

Thus, the main differences between the biconical and the two other traps are:

a) more frequent landing on the upper cone (white netting) which was not observed on the two other traps

b) a very high frequency of the behaviour "alighting" while in the two other traps the dominant component was "direct entry".

In summary, the following patterns were observed:

- Alight and finally enter: 49% on the biconical trap, 18.7% on the pyramidal trap and 18.1 % on the Vavoua. On the biconical trap, up to 74 % of the landings took place on the lower blue cone ; 12.8% landed on the black internal target and 6.8% on the white upper cone.
- Enter directly: 12.1% on the biconical trap; 56.2% on the pyramidal trap; and 59.1% on the Vavoua. Flies entered directly through the openings of the lower blue cone.

When they alighted (behaviour no. I) it could take only half a min., on average, to enter (Table 11). This duration was consistent. When flies alighted on the lower cone it took less time to enter if they performed some short flights, perhaps to investigate the position of the opening (± 10 seconds). A high variation characterized behaviours which finally involved take-off. It took on average ca. 3 min. to alight, perform short flights and take off.

On the pyramidal trap, flies spent about half a minute before entering. The same was true whether the fly landed on the black wing or on the blue wing. However, most flies entered directly without delay, unlike on the biconical trap.

4.1.5 Distribution of *G. f. fuscipes* and role of rainfall

4.1.5.1 Distribution of *G. f. fuscipes*

Taylor's power law was used on samples obtained from traps placed at 16 sites on 18 sampling occasions during the dry season (August). For male flies, $\log s^2 = 0.332 + 0.913 \log \text{mean}$ ($r = 0.85$). The value of "b" was 0.91, indicating a tendency of regular distribution in the field (Fig. 10). The ratio variance/ mean was in the range 1.8-2.2, which corresponds to a regular dispersion where the variance remains relatively equal under changing densities of flies. This is a comparison between the riverine thickets which were selected as potential tsetse sites, and not a random collection which could lead to an excess of zero catches contrasting with patchy catches in bushes (Poisson distribution).

The mean catch of females was related to the variance with the equation

$$\log S^2 = 0.372 + 1.092 \log(\text{mean}); \ (r = 0.899).$$

The value of the value of "b", Taylor's crowding index was 1.092. This value is expected for insects which do not swarm, but disperse in a random fashion, and for which the trapping probability does not vary systematically. However, the variance will increase faster with the density for females than it does for males; which suggests that more samples are needed to study females than males. Though, the difference expected between the two sexes in this regard is small.

4.1.5.2 Rain as a factor of dispersal

Rains are usually heavy in this equatorial region when they occur. The effects of rainfall on the total catches of *G. f. fuscipes* was investigated at 8 different sites on Rusinga Island. Catches were compared before and after rain.

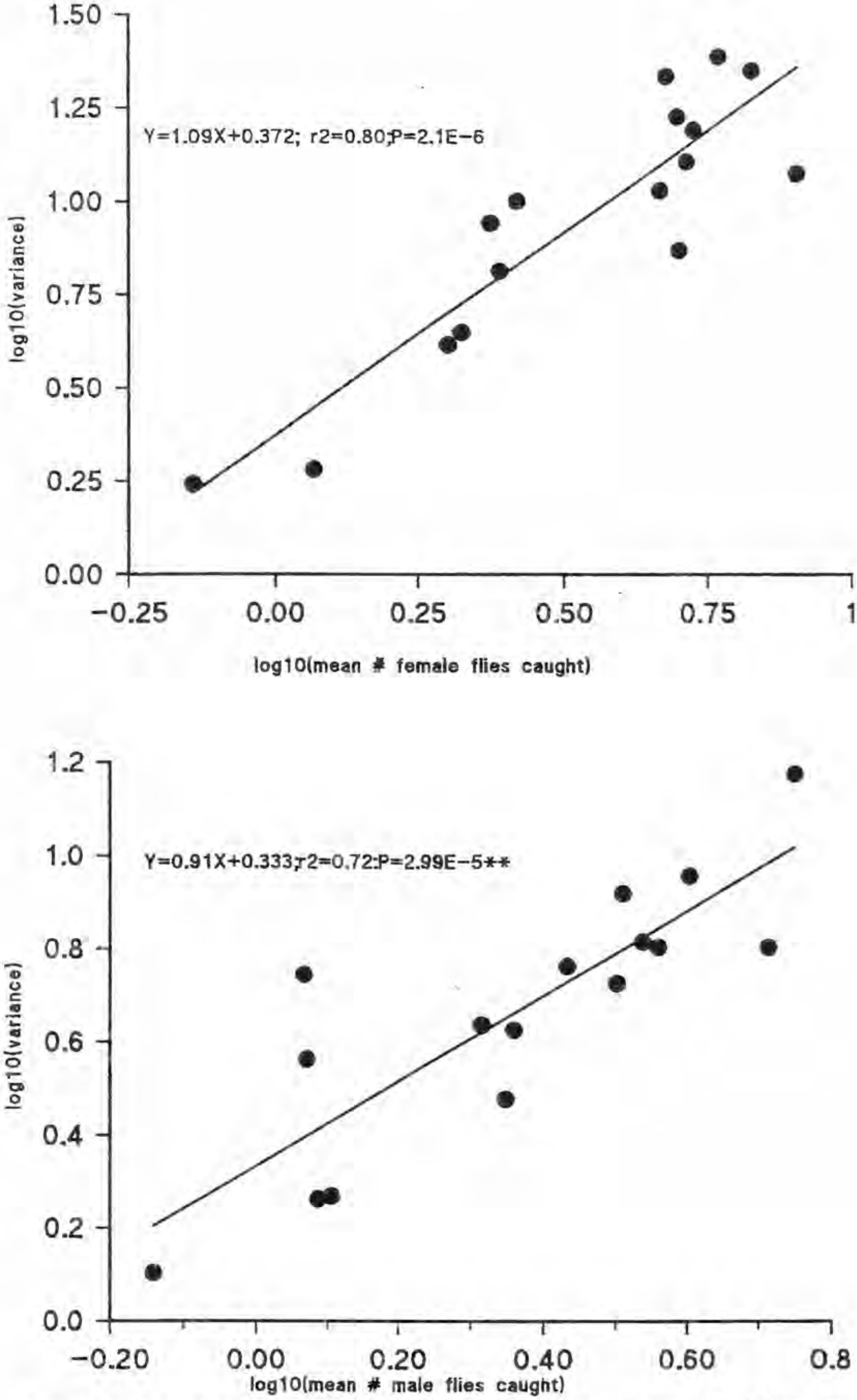


Figure 10: Tailor's power law as applied to (i) female and (ii) male *G. f. fuscipes* (18 sampling occasions at 16 sites).

An increase of mean catches was observed at 50% of the sites, though significant only at 2 sites. Elsewhere, there was a slight change (Fig. 11). Rain as a factor explained as much as 87% of the total variation of the numbers caught, respectively $R^2 = 61\%$ and 87% at the 2 sites where there was a significant difference between the catches before and after rain ($P = 0.02$ and $P = 0.006$). It is only at three sites out of eight that the amount of the variance accounted for was lower than 22 %. The data suggest that rain may be an important factor immediately effecting the fluctuations of catches of G.f.fuscipes.

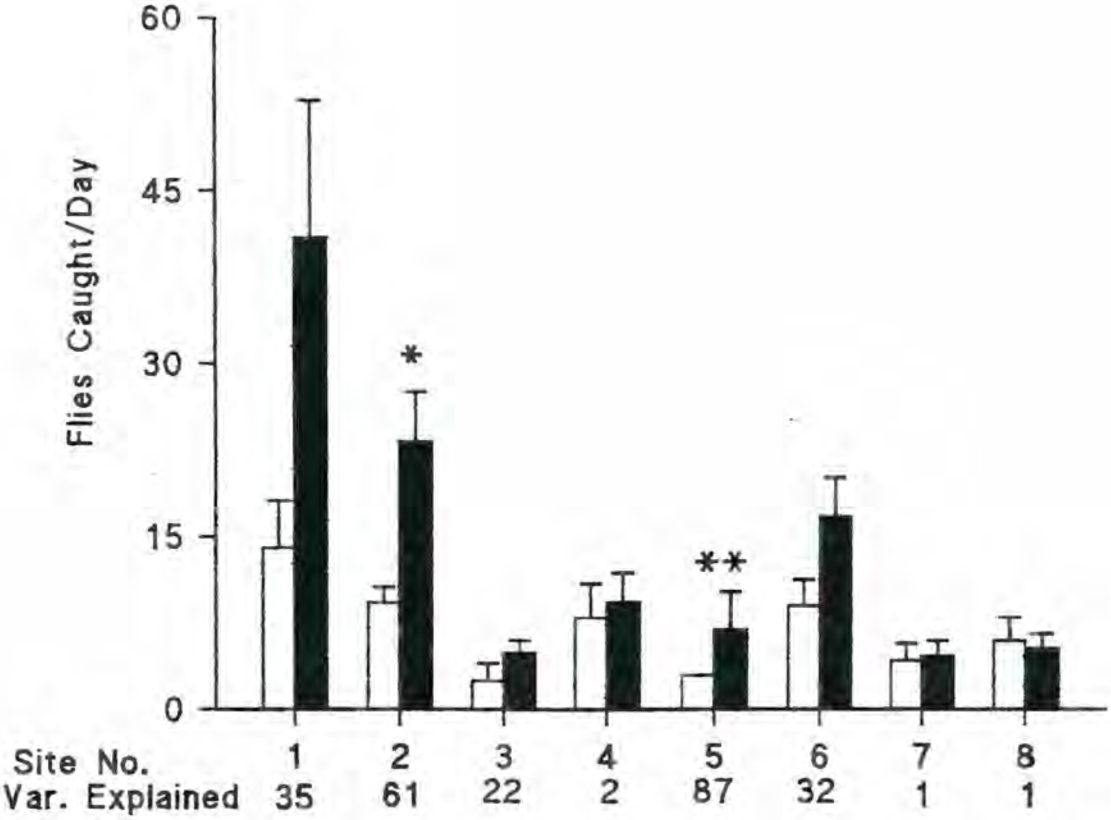


Figure 11: Changes of the abundance of *G. f. fuscipes* at trapping sites after heavy rains (30-35 mm) from 28 October to 2 November 1995 on Rusinga Island. Catches in standard biconical traps (n = 3-5); * for P = 0.02; ** for P = 0.006.

4.2 Responses of *Glossina f. fuscipes* to the Nile monitor lizard

4.2.1 Body zone preferences of *G. f. fuscipes* on *Varanus niloticus*

4.2.1.1 Frequency of landing on body zones

G. f. fuscipes showed a significant preference for the neck (Fig. 12), especially the nape of the neck of the Nile monitor ($P < 0.05$); 29.4% of the landings occurred on the neck; The head was the second preferred zone (11.6 %) for landing. The distal part of the tail practically accounted for no landings. There were more landings on the neck than on the whole back of the monitor lizard, from the shoulder to the pelvic region (24%). Yet, the back represents ca. 46 % of the upper area of the Nile monitor, while the neck is on average 9% of the area, the head 4%, the femoral part of the limb ca. 4% and the tibio-tarsal part of the leg ca. 4%.

4.2.1.2 Time spent on body zones and frequency of feeding

It is known that insects spend more time on body zones where they tend to feed (means fed: 4.78±0.76 min. ;not fed 2.36±0.67 min.; $P = 0.0024$; $n = 29\text{-}52$). *G. f. fuscipes* spent consistently (lower variance) more time on the neck; on the head the mean duration was similar to that spent on the neck, but with a remarkably high inconsistency alike the mid back (Table 14).

4.2.1.3. Morphological basis of body zone preferences

The largest scales were on the top of the neck (ca 5.9 mm^2) and on the tibio-tarsal region (5.1 mm^2) (Table 13). No significant difference $P<0.05$ occurred between sizes of scales on the head (4.1 mm^2), on the back (3.2-4.6 mm^2) and on the femoral region of the limbs (4.9 mm^2). The smallest scales occurred on the tail (1.3-2.5 mm^2).

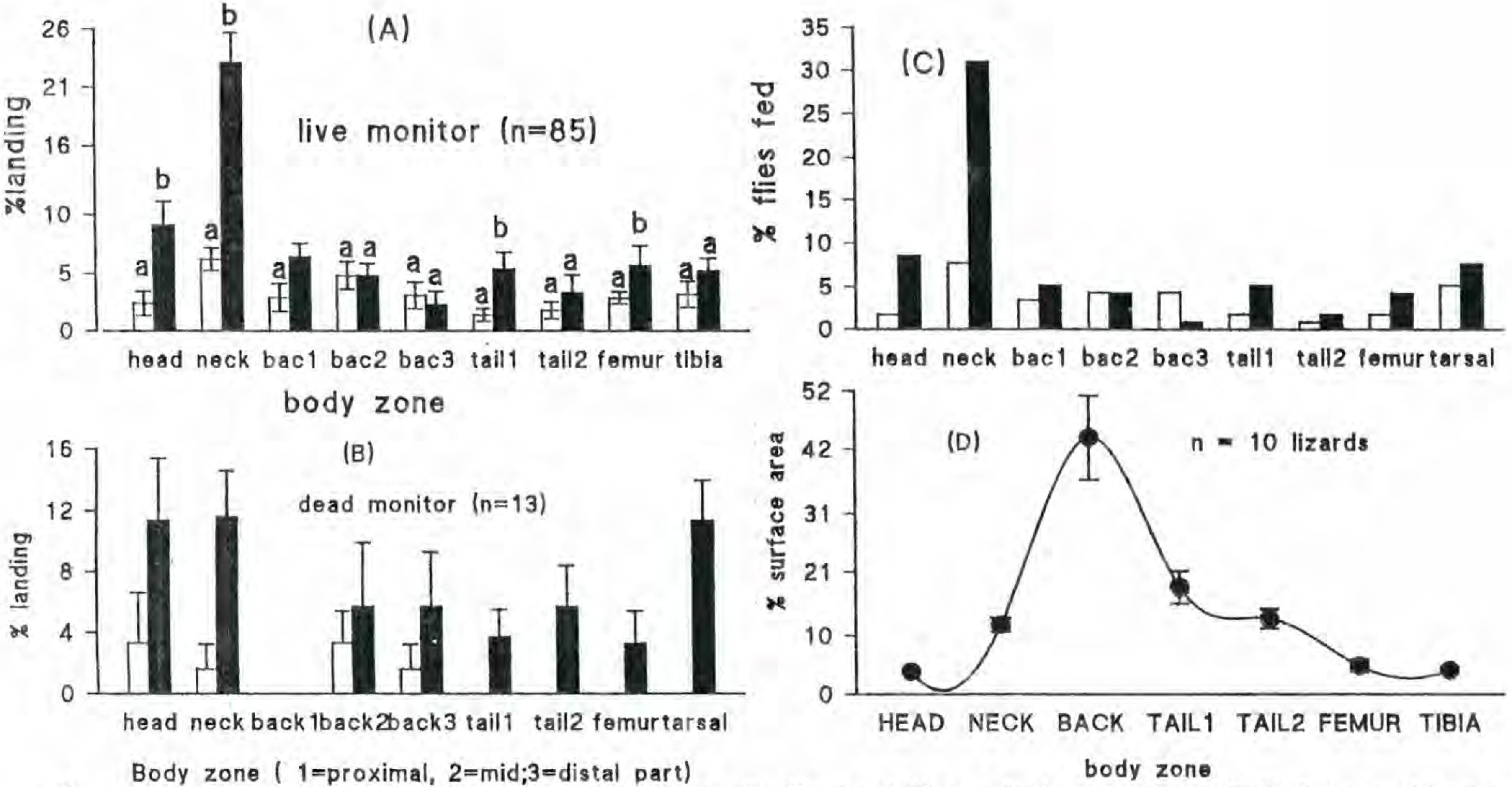


Figure 12: Body zone choices of *G. f. fuscipes* on (A) a live monitor lizard and (B) on a dead monitor lizard; (C) Preferences of feeding sites. Open bars indicate caged lizard under shade and solid bars for direct sunlight; different letters on top of a bar indicate significant difference ($P < 0.05$) within a body zone. Only the neck was highly signif. different from other body zones ($P < 0.01$). (D) % surface area covered by body zones of the Nile monitor susceptible to tsetse bites

No difference appeared in the thickness of the skin of the Nile monitor from all of the body zones; ca. 0.5 mm on average everywhere. However, the largest distances between scales were found on the femoral and on the tibio-tarsal regions of the limb, on the neck and on the shoulder.

Table 12: Time spent by *G. f. fuscipes* on various body zones of the monitor lizard

Body zone	n	duration ± SE (min.)
head	8	4.3 ± 2.52
neck	27	4.4 ± 0.92
back1	10	1.9 ± 0.60
back2	5	2.2 ± 1.95
back3	6	4.2 ± 2.19
tail1	4	0.4 ± 0.22
tail2	2	1.5 ± 1.48
femur	4	0.6 ± 0.46
tibia	10	2.6 ± 1.07

Table13: Morphological characteristics of scales on the monitor lizard, *V.n.niloticus*

body zone	shape of scale	area of scale (mm^2)	distance bet. scales (mm)	thickness of skin (mm)
head	polygonal	4.1±0.73	0.4±0.12b	0.4±0.03
neck	elongate	5.9±1.96	2.8±0.52a	0.5±0.10
back1	pyramid	4.6±1.02	2.3±2.00a	1.8±1.39
back2	polymorph	4.6±0.73	0.5±0.11b	0.4±0.05
back3	polymorph	3.2±0.55	0.3±0.00b	0.5±0.07
tail1.	rectangular	2.5±1.61	0.5±0.10b	0.4±0.10
tail2	rectangular	1.3±0.22	0.2±0.04b	0.5±0.03
femur	round	4.9±0.75	3.0±0.20a	0.5±0.05
tibia	tectiform	5.1±0.53	3.0±1.05a	0.5±0.06

letters different = signif. differencewithin a column;
no letter= no signif.diff. within the column; (n=10)

Elsewhere, including the head, scales were very close or even juxtaposed. This spacing of scales will effect the feeding-response as blood-sucking relies on the ease to insert mouthparts through the integument between scales.

4.2.2 Factors that effect landing and feeding behaviour

4.2.2.1 Effect of sunlight on landing

Significantly ($P < 0.05$) more flies landed on the monitor lizard under direct sunlight than in shade. There was no significant difference between the latency of the landing response under direct sunlight or in shade, although the sample size may have obscured the fact. More flies fed under direct sunlight than in shade (Table 14). Responses to body zones were not affected by light in a similar manner. There was a significant difference ($P < 0.05$) between the intensity of the landing response in shade and under direct sunlight , respectively on the head , on the neck (6.3% vs 23.1%), on the femoral region of the leg (2.9 % vs 5.8 %) and on the tibial region of the limb. The most dramatic change occurred on the head (mean 2.5% vs 9.1%). On all other body zones there was no significant difference between the intensities of the landing responses under direct sunlight and in shade. Although a slight increase was observed even in those regions. The pelvic region of the back was the only part of the Nile monitor where the landing response decreased with direct sunlight. On the mid back, the response remained consistently unchanged with direct sunlight.

It is suggested that reflectance plays an important role in eliciting the landing responses of *G. f. fuscipes* on the monitor lizard. To verify the importance of visual stimuli, I investigated the landing response on a dead , defrozen Nile monitor (ca 10 °C). Again, the highest landing response occurred on the neck and on the head and on the tibio-tarsal regions of the limb, with a significant increase ($P < 0.05$) in direct sunlight. As compared to responses to a live Nile monitor, the neck did not attract more flies than the other body zones under shade; and the variances were increased overall, suggesting the absence of another factor which could stabilize the choices of landing-sites.

The body zone choice is seemingly triggered by a visual stimuli (differential reflectance of the body zones, due to the changing geometry of scales). Another stimulus determines the amplitude (intensity) of the landing response; Likely it is skin temperature because the dead model was cold during the experiment.

4.2.2.3 Influence of light on the feeding response

Under direct sunlight, the feeding response tremendously increased on the neck (4 times), on the head (5 times) and was reduced 5 times on the pelvic part of the back (Table 15) as compared to tests under shade.

Table14 : Intensity of overall landing and feeding responses of *G. f. fuscipes* under shade and under direct sunlight. Latency (min.) indicates time elapsed before landing.

light status	n	landing/10	feeding/10	latency
shade	36	2.7±0.27a	1.1±0.22a	4.0±0.61a
sun	46	4.2±0.32b	1.6±0.23a	2.9±0.47a

Table 15: Number of flies which fed on the different body zones of the Nile monitor under direct sunlight or in shade (total = 116 flies)

zone	shade	sun
head	2	10
neck	9	36
back1	4	6
back2	5	5
back3	5	1
tail1	2	6
tail2	1	2
femur	2	5
tibia	6	9

Table16: Frequency of horizontal and vertical positions of *G. f. fuscipes* on the monitor lizard *V.niloticus* or flies which fed or did not feed when they landed

position and action	frequency	percent of action
vertical not fed	11	28.2
horizontal not fed	28	71.8

but also 3 times on the proximal part of the tail. Elsewhere, the change was a factor 1-2.5. The strong reductions on less attractive body zones compensated the strong increases on other body zones. It could not just be a question of light threshold, because tsetse are reared in lights lower than in this experimental box.

The trend of the feeding response was very similar to that of the landing response, and perhaps some low-volatility molecules on the skin are involved, in conjunction with reflectance, in the discrimination of body zones. This assumption was supported by the results of an experiment where I have given to the fly the choice to land on any part of a perforated PVC tube containing a live Nile monitor.

Flies consistently landed on holes between 0-5cm from the side where the head was positioned (29-66% of the total) (Table 17). Given the fact that the investigation by the fly was very negligible (my observation) and that *G. f. fuscipes* tended to remain on a body zone where it landed, feeding-sites were related to landing-sites. Also, the relationship between solar illumination and intensity of the landing was significant ($r = 0.75$; $P = 0.04$). Fly position upon landing whether vertical (in the direction snout tail) or horizontal (facing the side) was not clearly related with the feeding rate (Table 16).

Gas chromatographs of samples (Fig. 13) from very attractive zones (neck, head) and zones rarely fed on during the experiment (back, tail) showed that 4 of the active compounds identified by the Chemical Ecology Department (ICIPE) were only on the head (coded A, B, D, E;the real names and structures are part of a study in the chemical Ecology Department, ICIPE). Only A, undencanal, was present in all samples.

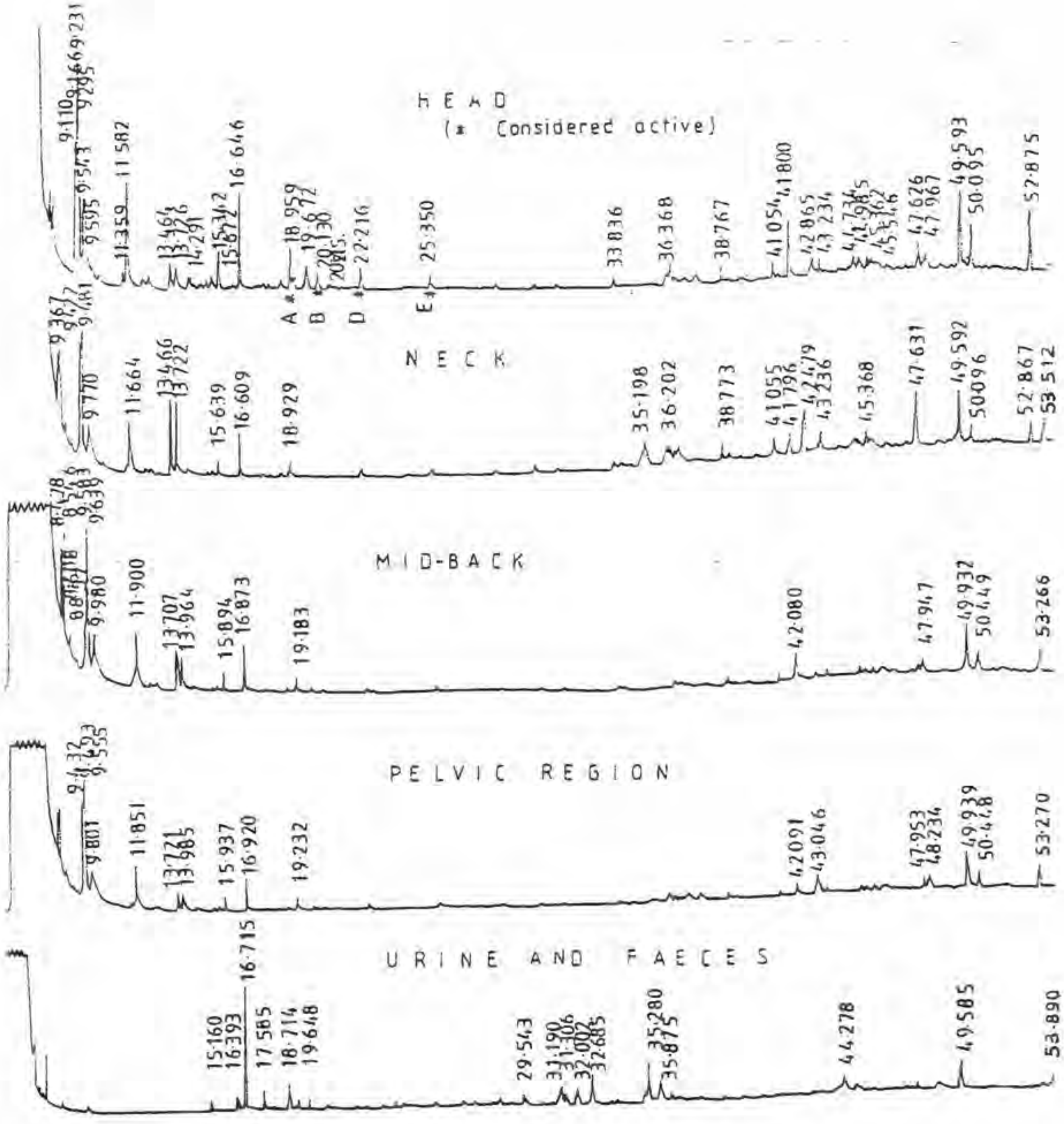


Figure 13: Chromatographs of hexane swabs from 5 Nile monitors. * and letters indicate compounds which chemists had found active for the antenna of *Glossina f. fuscipes*.

Table 17: Choices of positions on a perforated PVC tube containing a monitor lizard (n = 21-23)

position	5-10	10-15	15-20	20-25	25-30	30-35
landing (%)	28.6	0.0	9.5	14.3	0.0	4.8
	52.2	0.0	0.0	0.0	0.0	0.0
position	35-40	40-45	45-50	50-55	55-60	55-60
	14.3	9.5	0.0	0.0	14.3	4.8
	8.7	0.0	0.0	17.4	4.3	8.7

The neck was the most attractive body zone (this study) but those attractants occurred mostly in the sample from the head. It could be postulated that B, D, E emanate from the breath of the Nile monitor, sending traces on the head around the nostrils and snout. These compounds, except for A (undecannal) were absent from the urine of the Nile monitor. Undecannal, originating from diverse sources (breath, skin, urine), seems to be dominant among the active emanations of the Nile monitor.

4.2.2.3 Effect of temperature

Latency (min.) from resting to landing decreased from 13 min. to 1 min. as temperature varied from 28 °C to 31 °C. At 32°C-34°C, latency was minimal (ca. 0.5min.), suggesting that this temperature range of ca. 32-34°C is optimal for the attraction of *G. f. fuscipes* towards the Nile monitor. Above 35°C, latency increased towards the values of ca. 2-4 min. The fly's landing onto the monitor lizard was strongly activated by temperature. The fast response in the range 32-34°C shows that there is an optimal temperature to elicit the landing response. This range (32-34°C) of temperature corresponds to the eccritic temperature of this Nile monitor.

Activation of *G. f. fuscipes* by temperature (ambient) is illustrated by the strong relationship ($r=0.94$; $P < 0.01$) between the number of flies landing on the Nile monitor by session and the ambient temperature (Fig. 14). Below 28 °C, the landing response was very weak (0-1 fly per session), from 28°C onwards, at least 2 flies responded per session; up to 8 flies out of 10 could respond.

However, it is difficult to differentiate here whether it was the fly itself activated by temperature (as expected) or was it a factor from the lizard which may have been enhanced by temperature. Both together are likely to happen. The trend of

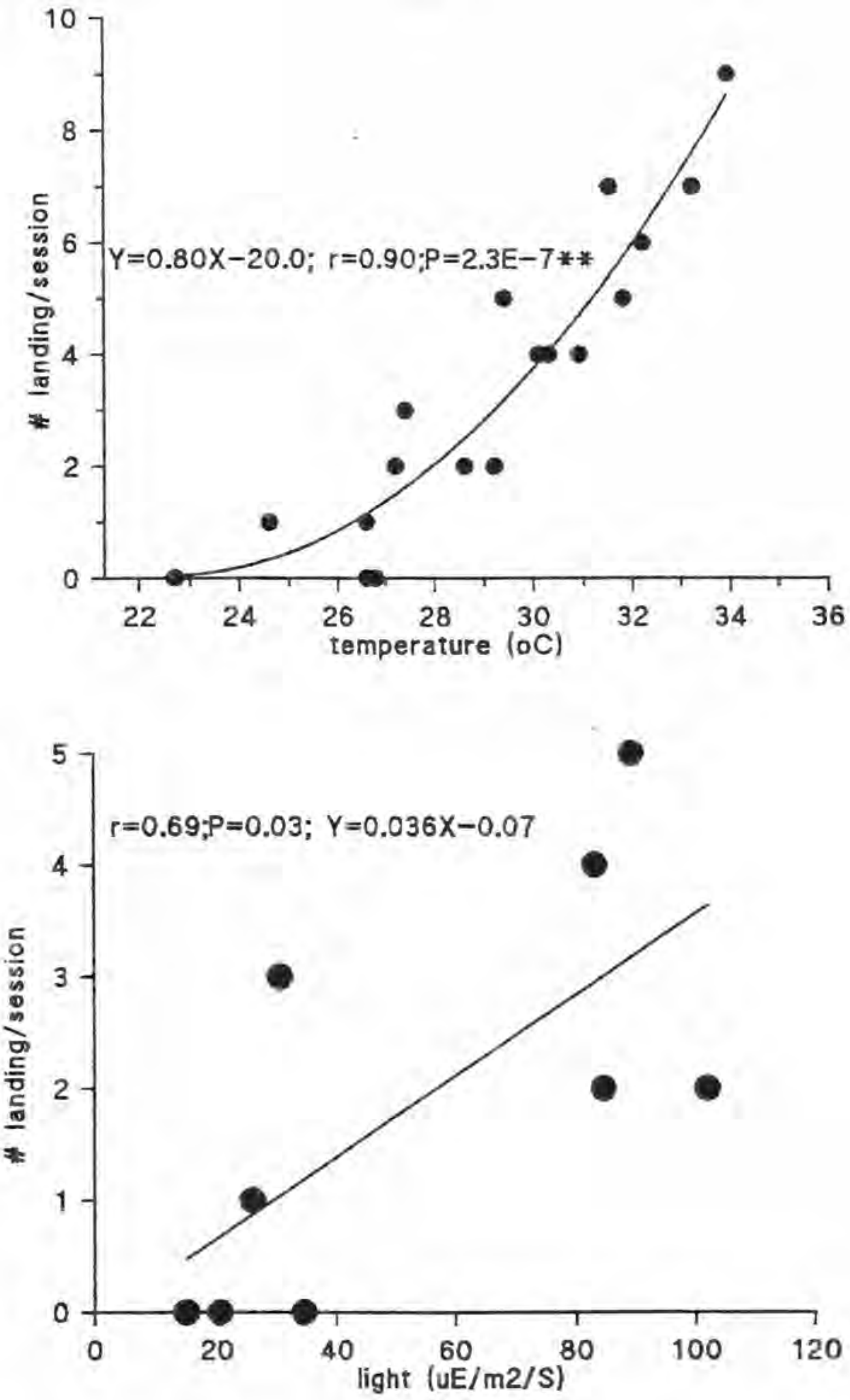


Figure 14: Relationship between the number of flies landing on the Nile monitor per experimental session of 15 min. and (i) temperature inside the cage or (ii) solar illumination.

the feeding response was similar to that of the landing response. The feeding rate was maximum in the range 30-32°C (Table 18).

4.2.2.4 Effect of captivity

The effect of the number of days spent by the lizard in captivity was analyzed. No significant difference was observed in the latency of the landing response, whether the lizard had spent 1-5; 5-10; 10-15 or 15-20 days in captivity . In all cases, 2.6-4.6 min. elapsed on average before the landing response started (Fig. 15). The same trend is observed for the intensity of the landing response. However, the highest rate of feeding was observed on Nile monitors which were caught freshly (1-5 days of captivity ; 2.5 flies/session on average), as compared to 0.6 flies/session in the class 5-10 days of captivity, 1.1 flies/session in the class 10-15 days and 1.8 flies per session in the class 15-20 days of captivity (Table 19).

The difference was statistically significant ($P < 0.05$) between the classes 1-5 days and the 2 classes 5-15 days; there was no significant difference between freshly caught lizards and those in long captivity (15-20 days). It suggests that, either the long captivity renders the Nile monitor tamed, tolerant and easy to feed upon, or is there a chemical factor which was reconstituted in the metabolism as the lizard got used to conditions of captivity. But, I could not observe any behavioural change with the duration of captivity. The Nile monitor remained sluggish and tolerant, at any stage of captivity, unless it was scared. Perhaps the assumption of a phagostimulant reconstituted could account better for that restauration of the feeding response.

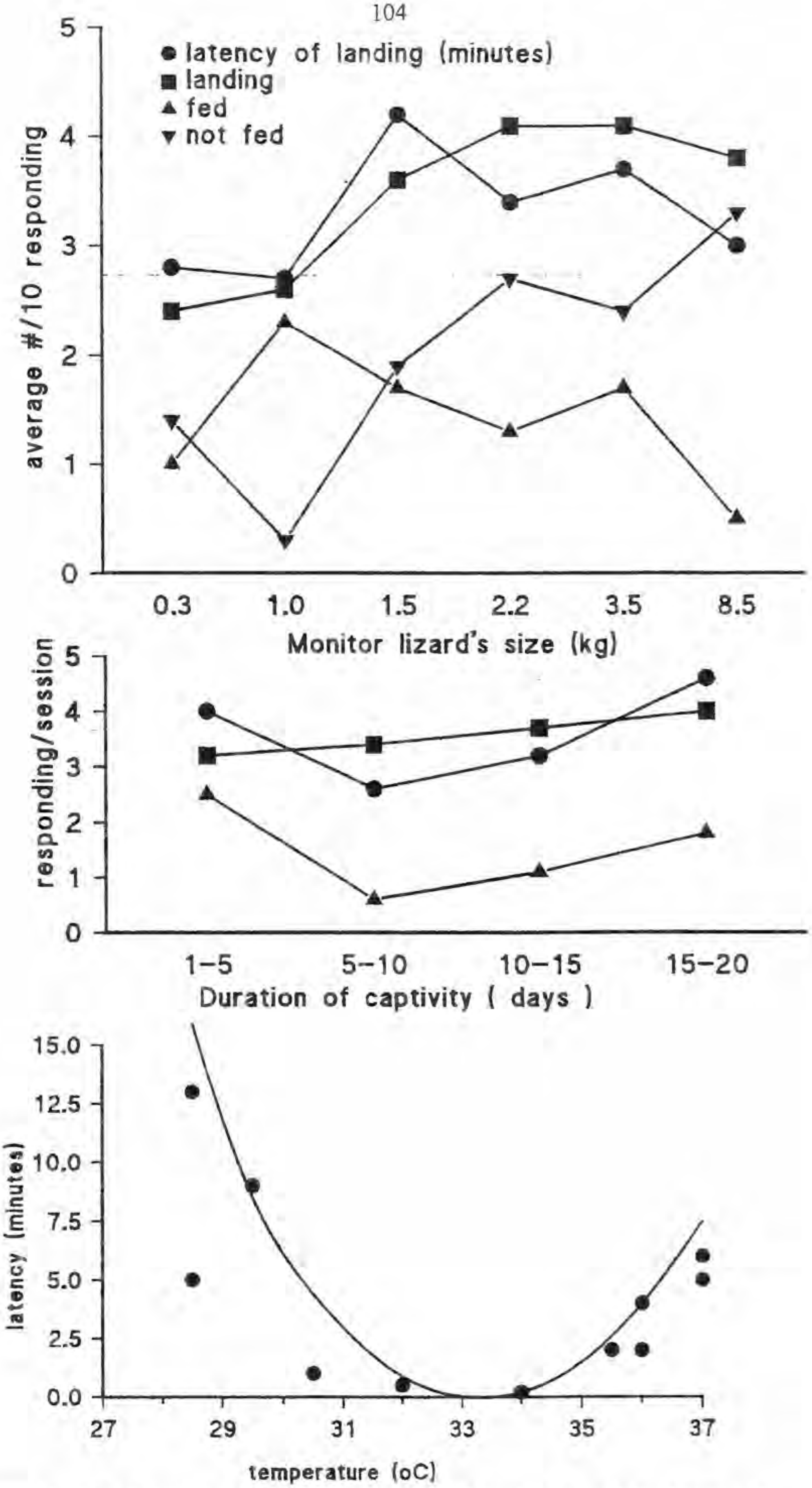


Figure 15: Effect of (i) size of Nile monitors and of (ii) duration of captivity on the responsiveness of *G. f. fuscipes;* (iii) Relationship between cage temperature and latency of the landing of *G. f. fuscipes* on the Nile monitor.

4.2.2.5 Effect of time of day

Assuming that an endogenous factor (a clock) regulates the diel activity of *G. f. fuscipes*, then it could be possible to find changes in the amplitude of the landing response with intervals of time (Table 20). The latency of the landing response did not change significantly when 1-hour intervals were split from 1100-1600 h (East african time). Latency remained consistent (3.5-3.6 min.); the same was true for the landing and the feeding response. However a slight peak tended to emerge on the curve at 1100-1200 and 1300-1400 h. Thus, it could be postulated that exogenous factors (light and relative humidity and host stimuli) accounted mostly for the activity of the fly for trapping and even for finding the Nile monitor as a host.

4.2.2.6 Effect of the size of the Nile monitor

There was no significant difference ($P < 0.05$) between the latency of the landing response whether the Nile monitor was 0.3 kg, 1.0, 1.5, 2.2, 3.5 (Table 21), or even 8.5 kg (range 2.7-4.2 min.). The same was true for the intensity of the landing

Table 18: Variation of the intensity of feeding of *G. f. fuscipes* on Nile monitors with temperature (°C). Same letter shows that there is no significant difference ($P > 0.05$)

temperature range (°C)	n	number fed/10
26-28	8	0.7±0.25 a
28-29	18	1.5±0.37 a
29-30	12	1.1±0.31 a
30-32	15	1.8±0.49 a
32-36	30	1.5±0.26 a

Table19: Responses of *G. f. fuscipes* to *V. niloticus* in relation with the duration of captivity

duration (days)	latency (min.)	landing (mean±SE)	fed	n
1 - 5	4.0±0.74a	3.2±0.45a	2.5±0.40 a	20
5-10	2.6±0.58a	3.4±0.43a	0.6±0.20 c	19
10-15	3.2±0.56a	3.7±0.38a	1.1±0.19bc	33
15-20	4.6±1.70a	4.0±0.81a	1.8±0.46ab	10

Table 20: Responses of *G. f. fuscipes* to *V. niloticus* with various time of day

time interval (local time)	n	latency	landing	fed
1100-1200	15	3.6±0.93a	4.1±0.59a	2.0±0.49a
1200-1300	26	3.5±0.70a	3.5±0.44a	1.0±0.19a
1300-1400	23	3.5±0.62a	3.2±0.34a	1.5±0.28a
1400-1500	12	3.6±1.32a	3.6±0.74a	1.7±0.54a
1500-1600	7	2.5±0.70a	3.7±0.68a	1.1±0.63a

Table 21: Effect of the size of the monitor lizard on the responses of *G. f. fuscipes*

size (kg)	n	latency (min.)	landing	fed
0.3	13	2.8±0.63a	2.4±0.52a	1.0±0.27ab
1.0	7	2.7±0.95a	2.6±0.71a	2.3±0.64 a
1.5	18	4.2±0.81a	3.6±0.47a	1.7±0.39 a
2.2	12	3.4±1.43a	4.1±0.67a	1.3±0.43ab
3.5	21	3.7±0.81a	4.1±0.46a	1.7±0.34ab
8.5	13	3.0±0.81a	3.8±0.52a	0.5±0.24 b

response. No significant difference was observed between the feeding rate on a very small lizard and a very large lizard (Fig. 15). The feeding success was very low on a very large lizard; the skin is hardened and difficult to pierce. On the other hand, there is a strong grooming response from the juveniles as opposed to the almost total tolerance of an adult Nile monitor, which sometimes even tolerated bites on the peri-ocular region. However, significantly less flies ($P < 0.05$) fed on very big lizard (ca 8.5 kg; 0.5 flies/session) as compared to lizards of 1.0 (2.3 flies/session) and 1.5 (1.7 flies/ session).

4.2.3 Availability of the Nile monitor as a host

4.2.3.1 Burrow and haul-out

Monitor lizards were observed coming out of hollows at the limit of the water-air interface of old dry trunks. The burrow had a submerged and an immersed part. This is where the big individual had spent the night. It was seen at haul-out-time at 0745hr on 28/6/1995. That day the sunrise occurred at 0735hr with a radiation intensity of 124.2 $\mu E/m^2/s$. It took 5 min. to climb up and settle 3 m up on the same tree trunk at the inflexion point of a branch bending West-East 30° and 45°. The skin colour was whitish-grey as it came from the burrow and drops of water were falling from the skin. The morning was overcast.

Monitor lizards flicker the tongue before coming out of the burrow. Upon haul-out, they inspect the surroundings, move back immediately into the burrow, or swim to a floating trunk or swim toward the lakeshore or immediately climb up on the same tree trunk on which the burrow is located. A big lizard was seen eating a crab at 0800 h just after haul-out. The handling lasted 7 min.

4. 2.3. 2 Pattern of the diel activity of the Nile monitor

I observed the basking behaviour of *V. niloticus* on a periodical colony of ca. 10 lizards, at an isolated thicket of *Aeschynomene elaphroxylon* (Plate 6). At 0900-1000 h (local time), most of the individuals were already basking on tree trunks (Table 22). The number of lizards basking remained almost constant until 1300-1400 h (Fig. 17) when they usually went back to water, or to burrows. This was the only one-hour interval when a significantly lower number of Nile monitors ($P < 0.05$) was observed at the site. At 1400-1500 h, the number of Nile monitors basking was back to the level of 0900-1000 h. A less significant decrease of the numbers was observed between 1500-1600 h, but most of the Nile monitors started leaving trees in the interval 1700-1800 h for the nightly rest in burrows. By overcast days, Nile monitors did not leave trees even between 1300-1400 h, until 1800 h when they moved back to burrows. Some rare individuals seen as late as 1930 h might have spent the night on trees.

I subdivided the behavioural repertoire of basking into 11 components (Fig. 16). The intensity of the act "high up flat on trees" was maximal from 0900-1200 h and 1500-1600 h (the latter less consistently). Nile monitors were basking intensively in these intervals of time. The act "high up oblique " was not frequent and it occurred mainly between 0800-0900 h by dull days, at almost all time intervals. Nile monitors, in this case, seemed to inspect their environment, perhaps for better basking prospects.

The act "moving upward on a tree trunk" was typical of the time interval 0800-0900 h; 1100-1200 h. Nile monitors did not simultaneously climb up on trees. Some individuals were late-comers. Most of the Nile monitors "moved downwards" from tree trunks at 1300 h and at 1500-1600 h. The highest intensity of the act "lying down

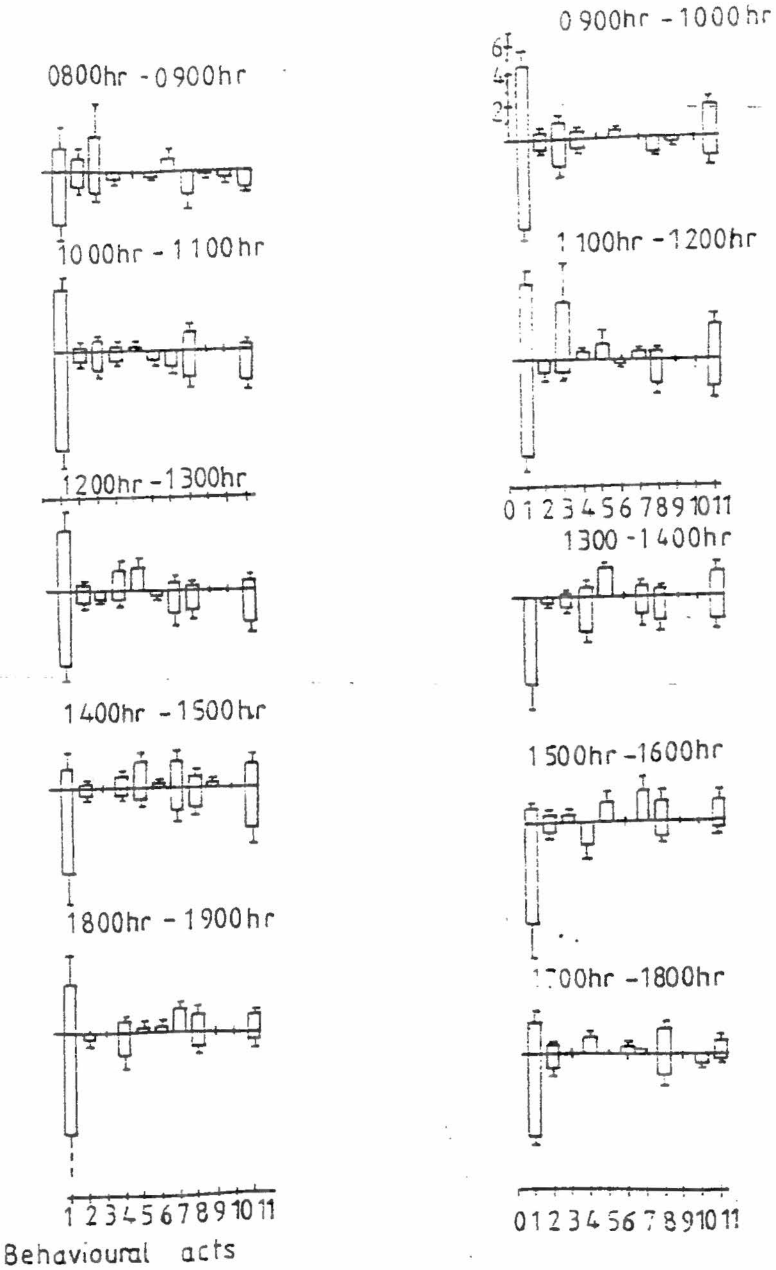


Figure 16: Repertoire of behaviours in a colony of ca. 10 Nile monitors at a site located within the littoral zone (plate 6) in July-August 1995 (n = 3-6). 1 = high up, flat, on trees; 2 = high up, head oblique, inspecting the environs; 3 = moving upward; 4 = moving downward; 5 = down under shade; 6 = swimming; 7 = down on land; 8 = on a floating log; 9 = coming out from the burrow.

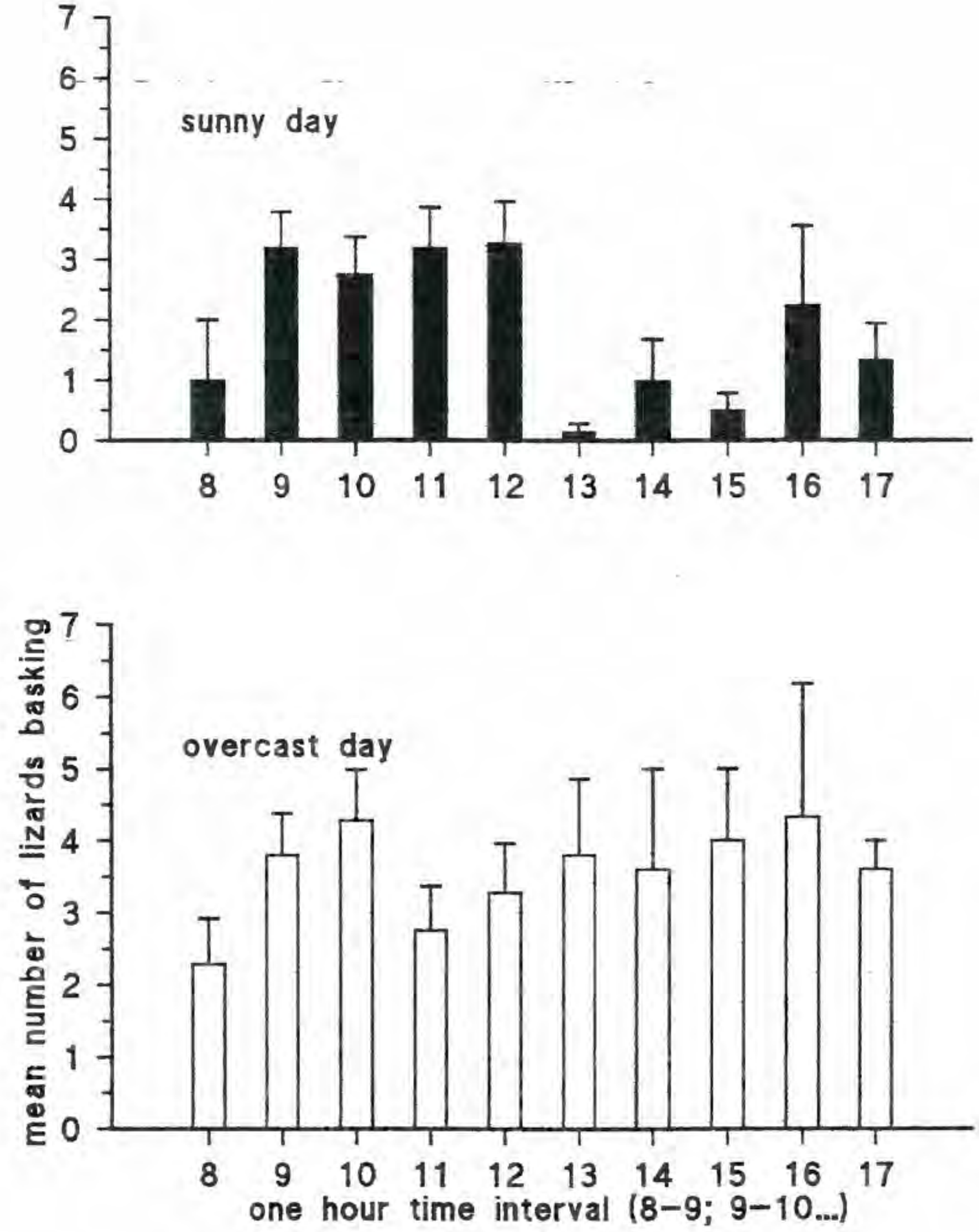


Figure 17: Nile monitor's intensity of basking (i) by sunny day and (ii) by overcast day.

in shade" was observed at 1400-1500 h and it could denote just a return for basking after the big interruption in the time interval 1300-1400 h. The act "swimming" had a very low intensity and frequency. Nile monitors did not hunt actively for fish in the waters around their basking-territory. Most swimming occurred as an attempt to escape from scaring objects, such as dogs, or to move from the littoral zone to the land. More Nile monitors were seen "down on land" between 1500-1700 h. It suggests that Nile monitors tend to hunt on the land after the long basking session of the morning and the long come-back to burrows at 1300-1400 h. By overcast days, more Nile monitors were seen on land (lakeshore) between 1200-1400 h. Mainly juvenile Nile monitors rest "on floating trunks". Some Nile monitors were seen "coming from burrows" at 0800-0900, 0900-1000 h and 1400-1500 h. This act was rarely recorded because burrows are hidden between trees. The same scarcity applies to the act "entering the burrow", which I saw only in the interval 1700-1800 h.

However, a high intensity characterized the act "positioned low on a tree trunk" which occurred mostly at 0900 h, 1100 h, 1300 h and 1400 h, suggesting a start of the basking after haul-out from the burrow or the end of a basking session to go back to the burrow. By sunny day, lizards moved back to burrows 2 hours after haul-out. At first, around 1100 h and again one hour after basking around 1300 h. These short stays in burrows can last 30-60 min.

The Nile monitor performed a bimodal pattern of activity by sunny days and a unimodal pattern of activity by overcast days. The trend of the basking activity in the morning from 0800-1300 h was very similar to that of the afternoon (between 1400-1800 h) (Fig. 17).

4.2.3.3 Body temperature of the Nile monitor and the need to bask

Many Nile monitors spend their night in burrowed logs inside water at the littoral zone of the Lake. In the morning, they come out to bask (haul-out). In an experimental situation, the cloacal temperature of a caged Nile monitor was 1.5 °C below the ambient at the onset of basking. The Nile monitor was exposed to direct sunlight and its cloacal temperature increased steadily until it reached ca. 32.5°C where it stabilized (Fig. 18). It was shown that under conditions with the normal local light regime, with weak wind, the Nile monitor basks for two hours to reach its eccritic temperature (33.0 ± 0.5). The body temperature rose at a rate of ca 0.08 °C/min (2 °C/25 min.) until the eccritic temperature was reached.

After basking, the lizard slowly lost the heat which was accumulated. After 100 minutes, it tended to be still 2 °C above ambient temperature (Fig. 19). The rate of cooling down was ca 0.05 °C/min. (1 °C ± 0.25/20 min). In this area, ambient temperature of 28 °C is common. Two hours after basking, the temperature of the Nile monitor was between 33.5-29.5 °C; but in nature, during the transition in water, the Nile monitor certainly loses more heat and gains water. It then needs a second basking session (bimodal activity pattern).

However, the relationship between body temperature and ambient temperature was very weak The Nile monitor directly absorbed solar energy to increase its temperature :

temperature = 0.0091 * (solar radiation) + 18.94; $r^2 = 0.95$; $P < 0.0001$).

Along most of the absorption curve, the increment rate was 0.01 °C/μE. Consequently, during a typical sunny day at Mbita area (western Kenya), the relationship between

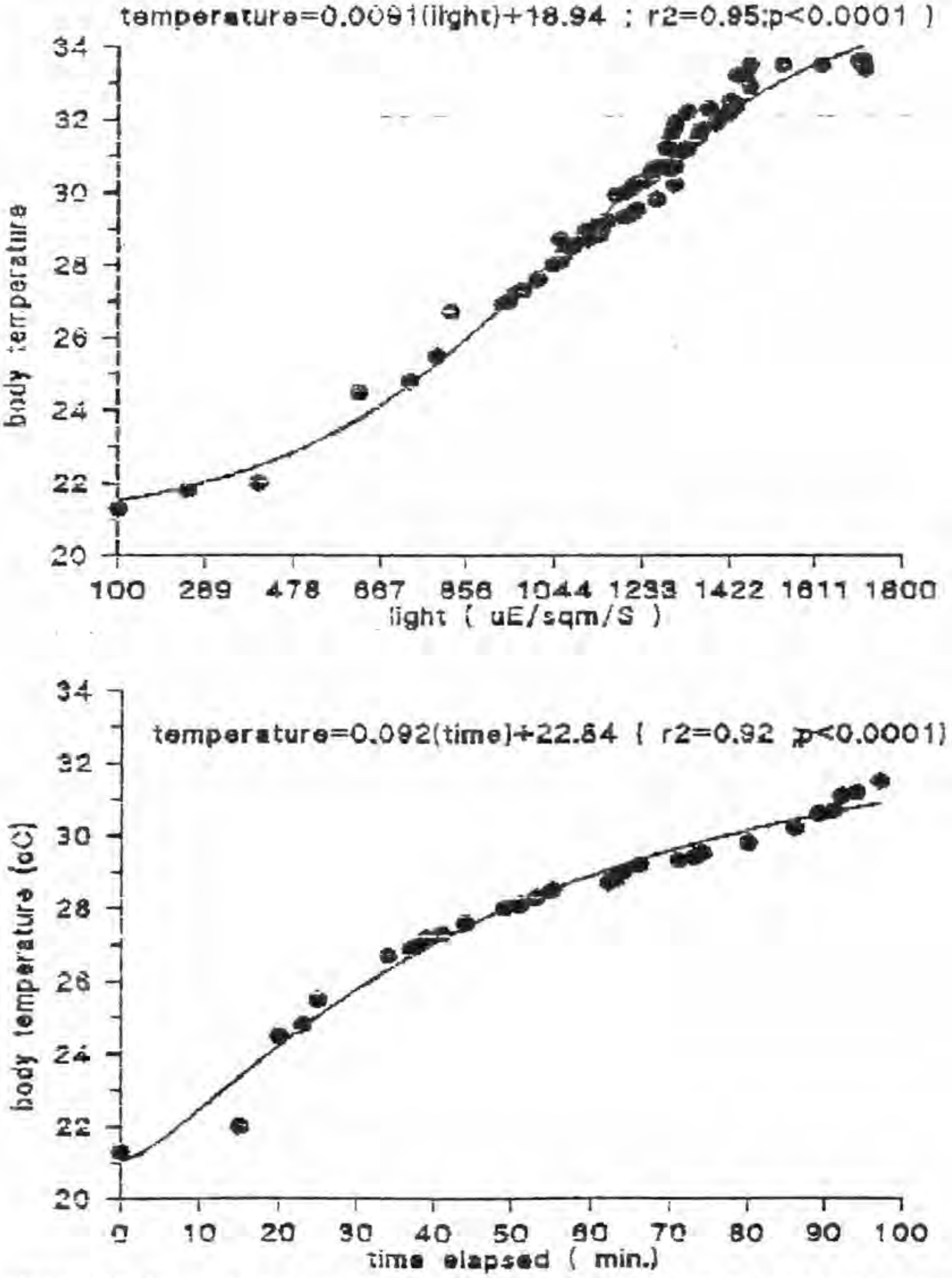


Figure 18: Increase of cloacal temperature of the Nile monitor during a basking-session (simulated in cage) in direct sunlight as a function of (i) solar illumination (not cumulative) and of (ii) time elapsed under the same conditions. Generalized from 5 monitors.

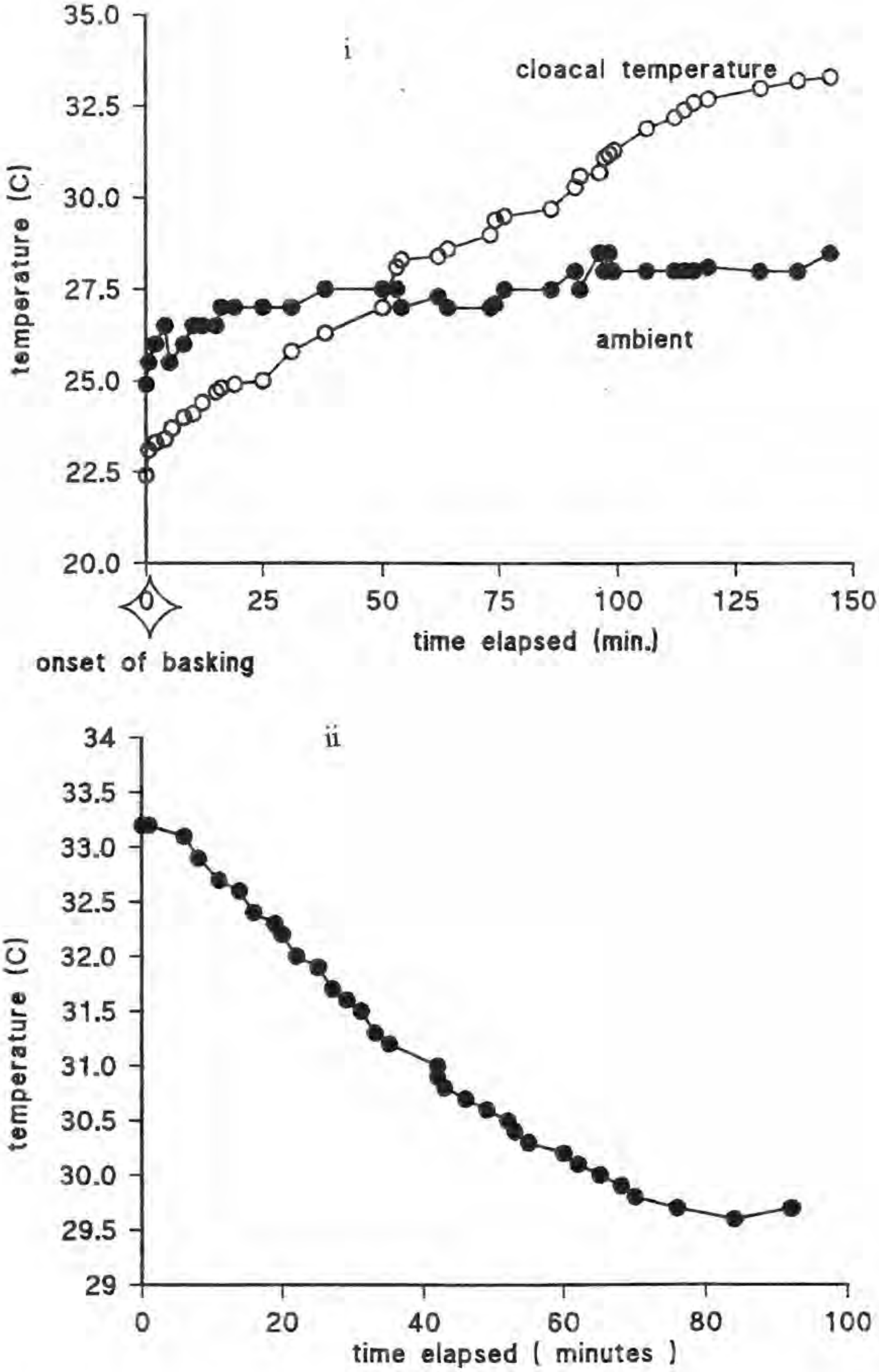


Figure 19: Pattern of cloacal temperature of the Nile monitor as a function of time (i) while basking or (ii) cooling down under shade (n = 3 monitors).

duration of basking and body temperature will be very strong ($r^2 = 0.92$; $P < 0.0001$); but the strong wind at the lakeshore (> 2m/s) will slow down the increment of temperature at a basking session. Thus, the lizard could bask more than two hours to reach its eccritic temperature; So, while a massive midday haul-in could have been expected at ca. 1200 h (time of emergence ca. 1000 h), it occurs instead at ca. 1300 h.

Table 22: Number of monitor lizards observed by sunny or by overcast days on a colony of ca. 10 specimens at Mbita (western Kenya) (n=3-6)

local time	overcast day	sunny day
0800-0900	4.7 ± 2.13	3.5 ± 0.50
0900-1000	6.5 ± 0.50	5.4 ± 1.16
1000-1100	9.3 ± 2.60	5.0 ± 1.08
1100-1200	8.0 ± 0.00	6.4 ± 0.60
1200-1300	7.7 ± 2.02	5.4 ± 0.81
1300-1400	10.0 ± 1.00	3.7 ± 0.60
1400-1500	8.5 ± 2.50	5.8 ± 0.54
1500-1600	6.5 ± 0.50	4.5 ± 0.95
1600-1700	6.6 ± 1.45	5.5 ± 1.50
1700-1800	5.6 ± 0.92	4.0 ± 0.44
1800-1900	4.2 ± 0.47	6.0 ± ?

4.2.3.4 Height and angle for basking

The Nile monitor preferred sites with bent, dry logs (Fig. 21). The modal number of Nile monitors at a site was 1.0 (Table 25), but juveniles could be found in numbers reaching 6. A colony of as many as 10 Nile monitors occurred at sites with plenty of bent dry logs, in littoral zones at ca. 20 m from the lakeshore. At such a site, they were observed without any tendency to escape.

Many monitor lizards (ca 60 % basked at heights between 0-2 m; about 35% basked at heights between 3-4 m (Table 23). However, some Nile monitors were seen basking at heights of 4-7 m (ca 5%). The most favoured angle for basking was ca. 45° (40.5% of the observations; Table 24). A proportion of 28.6% basked at angles of ca. 30°, and even lower (10°; 30.9%), especially juveniles which could not compete for the best basking sites. However, the size of the lizard was not significantly related to the basking height ($P = 0.15$). But the height of basking was determined by the need to find an appropriate angle ($P = 0.02$); and the angle was perhaps more important than the height (Table 26). The choice of the basking-angle was significantly related to the size of monitor lizards ($P = 0.05$).

Table 23: Estimated heights at which arboreal monitor lizards bask at Mbita (western Kenya); n = 52

height (m)	0.5	1	2	3	4	5	6	7
frequency	12	5	13	12	7	1	1	1
percent	23.1	9.6	25.0	23.0	13.4	1.9	1.9	1.9

Table 24: Estimated angles formed by logs on which monitor lizards bask at Mbita (western Kenya) n = 42

angle	10	30	45
frequency	13	12	17
percent	30.9	28.6	40.5

Table 25: Number of monitor lizards basking at a same site (n = 43)

number	1	2	3	4	6
frequency	16	12	5	5	5
percent	37.2	27.9	11.6	11.6	11.6

Table 26: Effect of size on choice of basking-height, effect of height on choice of trunk's angle, effect of lizard size on the basking-angle, effect of number of lizards at a site on the basking-height, overcast or sunny day vs basking-height, overcast or sunny day vs basking angle

variables	n	df	likelihood ratio chi-square value	probability
size x height	35	21	27.38	0.158
height x angle	37	24	39.19	0.026
size x angle	28	9	16.82	0.051
number x height	38	28	40.11	0.065
light x height	52	9	10.37	0.321
light x angle		3	6.41	0.093

More juveniles were found down. The angle of basking is an important component of the biotope preference of the Nile monitor. If the dry, bent logs were to be destroyed or else if the ambatch were withdrawn from the farming-system here, the population of Nile monitors would be threatened. The ambatch, when it gets old, provides holes at the water-air interface which are ideal burrows for the Nile monitor; such a trunk is bent and nude, providing optimum opportunities for basking.

4.2.4 Spatial distribution and relationship weight-length of the monitor lizard

The relationship between the open area at a given site and the number of lizards found at the site was weak ($r = 0.43$; $P = 0.08$); Showing that lizard tends to be solitary and that the number at a site is not essentially limited by the area available (Fig. 20). However, the Nile monitor lizard favoured a corridor around its site as shown in this study. Tailor's power law gave a value of $b = 1.027$ for the Nile monitor. This value is very close to 1 for an animal like the Nile monitor which is obviously not gregarious.

The Nile monitor strikes very readily with its tail and teeth. Thus, it is useful for researchers to know the relation weight-length so that they can estimate the weight from the length and reduce the risks of handling the animal (Fig. 20). Also , size (weight) is related to the success in tsetse's blood-sucking.

For females and juveniles, the relationship weight (kg) -total length (cm) was:

$$\text{Weight} = 6.99\text{x}10^{-7} \text{ x TL }^{3.103} \ (r = 0.95^{**}).$$

Maximum weight of females was about 5.5 kg with a length of circa 160 cm. The relation weight - length of males could also be predicted by :

$$\text{Weight} = 0.041 \text{ x TL}^{0.997} \ (r = 0.96^{**}).$$

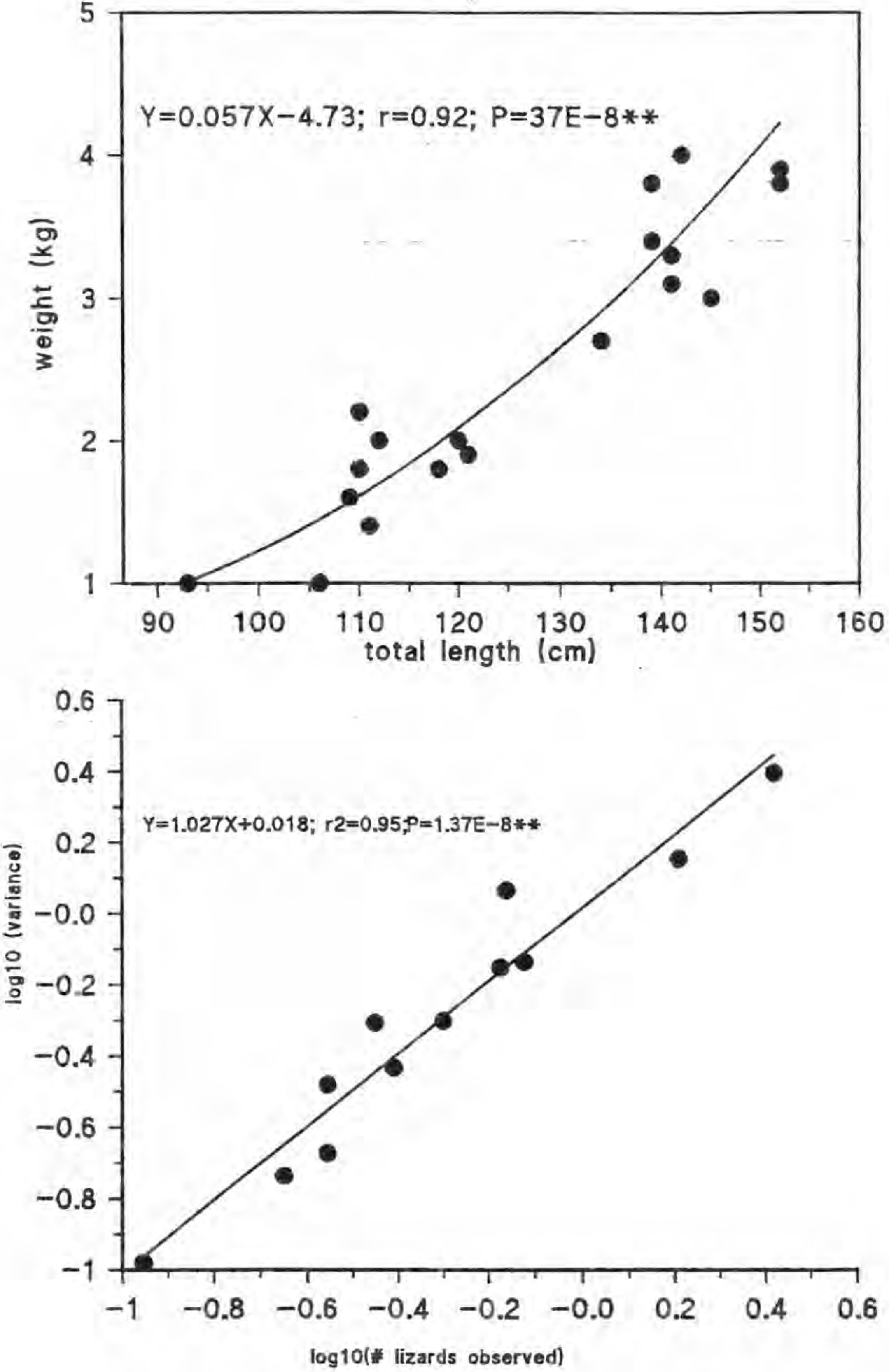


Figure 20: (i) Relationship weight-length for juveniles and mature females of the Nile monitor and (ii) Tailor's power law as applied to monitor lizards' distribution.

The maximum weight of males was ca. 8.5 kg and they reached a length of ca 190 cm.

4.2.3.5 Adaptive responses of *G. f. fuscipes* to Nile monitors in nature

Female flies tended to aggregate at sites where monitor lizards live (Fig. 21). The relationship between mean number of female flies caught in a biconical trap and the maximum number of monitor lizards found around those trapping sites was highly significant ($r = 0.67$; $P = 0.005$). The relationship was also significant for male flies ($r = 0.54$; $P = 0.03$). Given the usually very high ratios of females in catches, total catch was also significantly related to the number of monitor lizards at a site ($r = 0.57$; $P = 0.023$).

Landings in nature were observed on Nile monitors basking down (height = 0 m), or at heights of 2 m, 3 m and ca. 4 m. It was mostly by sunny hours between 0900-1700 h, mainly at ca 0900, 1100-1200 h, but also by overcast times (Fig. 22). It is likely that the intensity of the landing response to the lizard would just be proportional to the circadian activity of the fly. Flies landed on different body zones in nature, but the lizard in the bush was positioned in such a way that no reliable observation of the body zone preference could be done. Swarms were not observed around lizards. Usually one fly landed on the lizard (1.3 on average) at a time and the feeding took about two min.; the fly was engorged and took off. Some flies landed on the lizard and spent a whole hour without moving or even attempting to feed.

4.2.4 Does *G. f. fuscipes* find *V. niloticus* via anemotaxis?

The attempt here was to verify if *f. G. fuscipes* uses anemotaxis to find the Nile monitor when there is need to feed (Table 27).

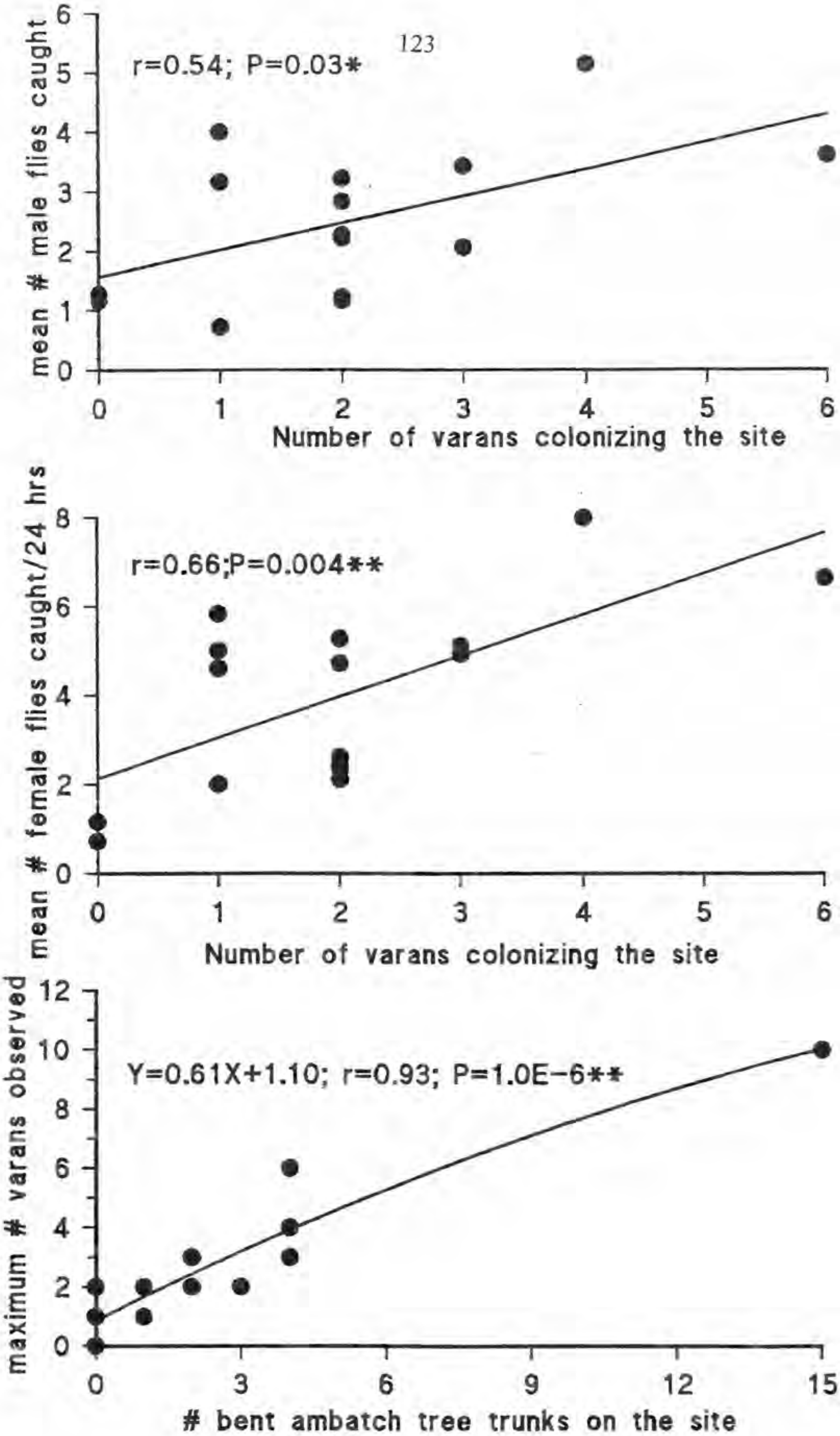


Figure 21: Relationship between (i) the number of male, (ii) female *G. f. fuscipes* and the number of Nile monitors colonizing the same site. (iii) Relationship between the number of bent dry logs of ambatch tree and the number of Nile monitors colonizing a given site (16 sites; 18 sampling occasions).

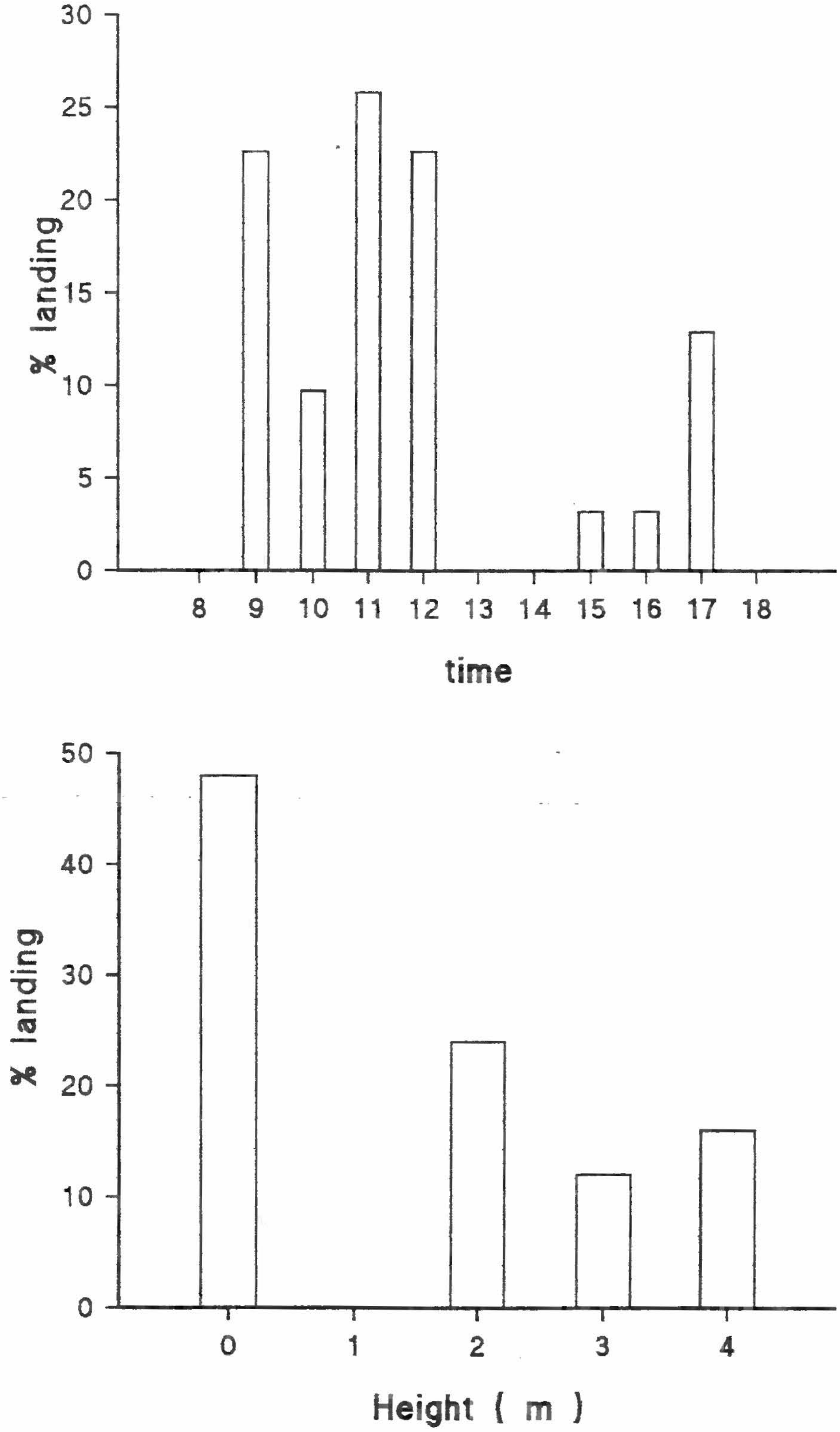


Figure 22: Proportions (%) of tsetse flies which landed on the Nile monitors in the field, in relation with (i) time of day and (ii) basking-height (n = 32 flies observed on 25 monitors).

4.2.4 1 Patterns of the response to whole body odours of a live Nile monitor

When the Nile monitor was present in the odour chamber (Table 28) of the experimental wooden olfactometer, only 32.5 % to 38.5 % of the flies were non-responders (Fig. 23). They remained in the release chamber. Thus, 61.5 to 67.5 % of the flies performed an upwind flight from the release chamber to the next compartment where further search for the host would occur. Only 4.2 to 15.8% of responders abandoned the search in the second compartment. Thus, from 84.2% to 95.8% of the responders continued the search. Of these, 7.7% to 30% (percentage of total responders) remained in the close-range chamber and did not reach the Nile monitor. But, as many as 21% to 53.5% of the responders reached the host.

4.2.4.2 Role of lizard shape and shadow

Two cases were tested: a stuffed Nile monitor to analyze the effect of shape alone and an empty cage to eliminate both visual and olfactory stimuli. When a stuffed lizard (Table 28) was present in the odour chamber, the proportion of non-responders ranged from 47.6 to 52.3%; thus the proportion of non-responders increased highly significantly ($P < 0.01$) as compared to when a live lizard was tested. The corollary was a highly significant decrease ($P < 0.01$) of responders (47.6-52.3 %). Among responders, significantly ($P < 0.05$) more flies abandoned search in the second chamber when a stuffed lizard was tested as compared to a live one (Fig. 24). The range of the proportions of responders which abandoned the search in the second compartment was 19.0-25% (9.4% as an extreme). However there was no significant difference between proportions of responders which remained in the close-range chamber without

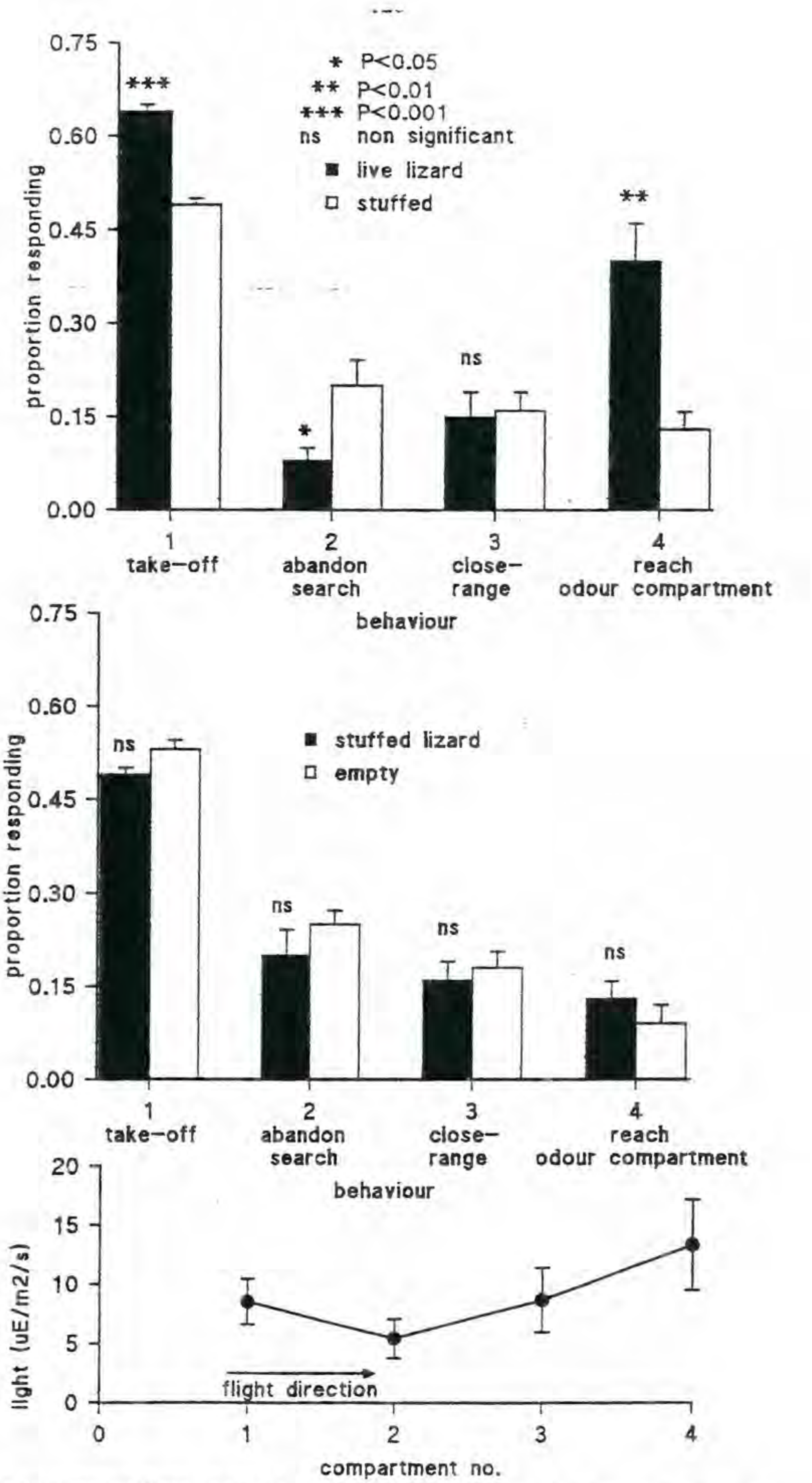


Figure 23: Upwind flight of *G. f. fuscipes* in a wooden flight chamber when (i) a live monitor lizard was present as compared to a stuffed monitor; (ii) when a stuffed monitor was present as compared to an empty odour compartment (119-131 male flies tested in 4 replicates). (iii) light conditions in the experimental cage.

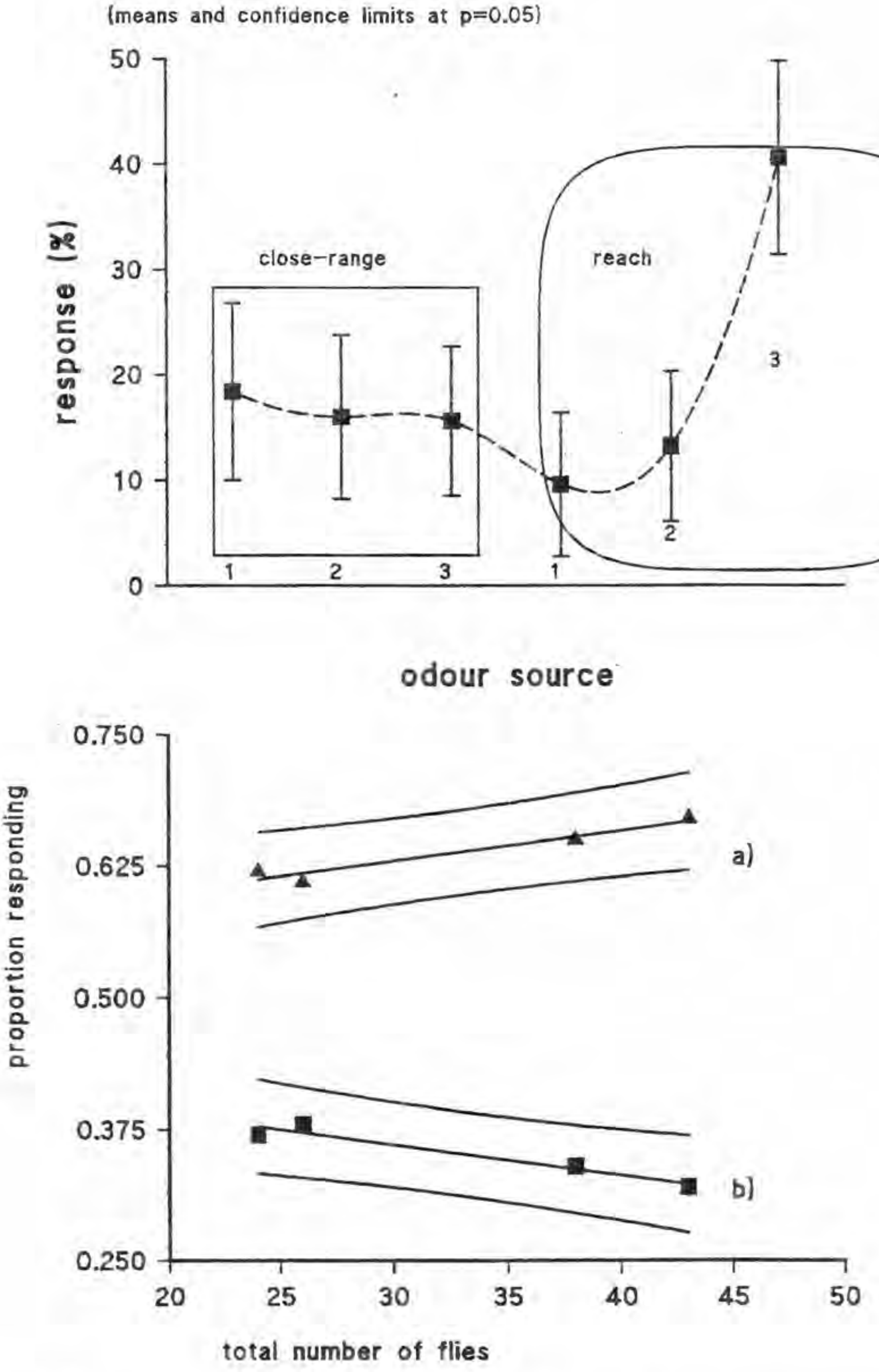


Figure 24: Responses at close-range and proportion reaching the odour compartment 1 = empty; 2 = containing a stuffed monitor lizard; 3 = containing a live monitor lizard; Relationship between the number of flies used during the experiment and (a) the proportion of flies performing anemotactic flight ($r^2 = 0.93$; P = 0.03; Y = 0.002X+0.54). (b) the proportion of flies which remained passive ($r^2 = 0.93$; P = 0.03; Y = 0.002X + 0.44).

attempting to land on a stuffed or on a live Nile monitor; the range was 8.3-22.6% in the case of a stuffed lizard.

A highly significantly lower proportion ($P < 0.001$) of responders reached a stuffed Nile monitor as compared to a live Nile monitor. Here the range was 14-16 % (which reached a stuffed lizard) while as many as 41.6-53.5 reached a live lizard. Thus, out of 100 flies which reached the close-range of the monitor lizard (average 40 % taken here as a maximum), approximately only 8.8 % could do so by using exclusively the shadow (shape) of the lizard, assuming that reflectance is negligible in shade.

Table 27: Counts from behavioural acts in the experimental wooden flight chamber.

Treatment	no. flies released	rep	numbers found in compartments release	search	close-range	odour chamber
live lizard	26	1	10	2	2	12
live lizard	38	2	13	6	11	8
live lizard	43	3	14	2	4	23
live lizard	24	4	9	1	4	10
stuffed lizard	53	1	27	5	12	9
stuffed lizard	21	2	11	4	3	3
stuffed lizard	21	3	10	6	4	1
stuffed lizard	24	4	12	6	2	4
empty cage	20	1	10	6	3	1
empty cage	29	2	13	7	4	5
empty cage	21	3	10	6	4	1
empty cage	35	4	15	7	9	4

Table 28: % responses to various odour treatments in the olfactometer

Odour status	total	Reps	release	search	close-range	odour chamber
live lizard	26	1	61	7	7	46
live lizard	38	2	65	15	28	21
live lizard	43	3	67	4	9	53
live lizard	24	4	62	4	16	41
live lizard		Mean	64	7	15	40
stuffed lizard	53	1	49	9	22	16
stuffed lizard	21	2	47	19	14	14
stuffed lizard	21	3	52	28	19	4
stuffed lizard	24	4	50	25	8	16
stuffed lizard		Mean	49	20	16	12
empty cage	20	1	50	30	15	5
empty cage	29	2	55	24	13	17
empty cage	21	3	52	28	19	4
empty cage	35	4	57	20	25	11
empty cage		Mean	53	25	18	9

It is suggested, here, that anemotaxis involving an odour trail plays a very significant role in the host-finding of *G. f. fuscipes* towards *V. niloticus*. I attempted to quantify the role of odour in this behaviour.

4.2.4.3 The role of wind, shape and shadow

An experiment was conducted with an empty odour compartment to estimate the role of wind and also to deduce the role of shape and shadow in reference to the experiment involving a stuffed Nile monitor. Under these conditions, 50-57 % of the flies responded. As many as 20-30 % of the responders abandoned in the search compartment and 13-25 % of the flies reached and remained in the close-range compartment. But, still 4-17 % of the responders reached the empty odour chamber.

4.2.4.4 Effect of fly abundance in the anemotactic behaviour

G. f. fuscipes does not swarm; thus, the assumption that the density of flies (number released in an experiment) could influence the anemotactic behaviour was tested (Fig. 24). When a live Nile monitor was in the odour chamber, a very strong positive linear relationship ($r^2 = 0.94$; $P = 0.02$) was detected between the number of flies released in the "release" compartment and the proportion that was to take off upwind (Table 29).

Further in the search, there was no significant relationship between the number of flies released and the rate of abandon of search ($P = 0.71$), the proportion that reached the close-range ($P = 0.81$) and the proportion which reached the odour compartment. When a stuffed lizard was in the odour compartment, no significant relationship was found between abundance of flies (number released) and respectively

Table 29: Parameters in the relationship between density of *G. f. fuscipes* (as number of flies used in the anemotaxis experiment) and the intensity of behavioural acts

LIVE LIZARD

behaviour	slope (b)	SE of slope	cv	r^2	Prob.
non-responders	-0.0029	0.00048	2.18	0.94	0.02*
take-off	0.0029	0.00048	1.21	0.940	0.02*
abandon search	0.0016	0.00390	78.16	0.080	0.71ns
close-range	0.0019	0.0073	74.48	0.030	0.81ns
reach	-0.0006	0.010	41.90	0.002	0.95ns

STUFFED LIZARD

behaviour	slope (b)	SE of slope	cv	r^2	Prob.
non-responders	0.0003	0.0008	4.74	0.05	0.76
take-off	-0.0003	0.0008	4.78	0.05	0.76
abandon search	-0.0040	0.0010	24.34	0.76	0.12
close-range	0.0025	0.0021	36.01	0.41	0.35
reach	0.0018	0.0022	46.36	0.24	0.50

the rate of responders (P = 0.76), the proportion which reached the close-range (P = 0.35) and the proportion which reached the stuffed Nile monitor (P = 0.50). However, a moderate negative relationship (r = -0.87; P = 0.12) was found between the abundance of flies and the rate which abandoned the search on the way.
There was a very strong negative relationship ($r^2 = 0.93$; P = 0.03) between the proportion of flies which responded (upwind flight) and the total number of flies involved in the experiment. A very strong negative relationship ($r^2 = 0.99$; P = 0.0035) was observed between the number of flies released and the proportion of responders that abandoned the search. Thus, *G. f. fuscipes* tends to disperse when the number of conspecifics increases in its strict surroundings. It seems that there is a lower threshold at which this "anti-swarming" behaviour starts. The number released had no effect at the close-range (P = 0.39) and "reach" levels (P = 0.27).

To avoid that phototaxis interfers with anemotaxis, the experiment was conducted in shade. Measuments of light energy indicate that there was no significant difference between levels of illumination (range: 5-13 $\mu E/m^2/s$) inside the four compartments; if it were by phototaxis, a flight from the release compartment to the search compartment could not have taken place (Fig. 23).

Out of 100 flies that took off from a long-range zone towards the lizard, approximately 50% did so by ranging upwind; This is consistently shown by the experiment with stuffed lizard and with empty odour cage experiment (respectively 51.9 and 49.5 % responders).

4.3. Attempts to improve the Challier-Laveissière conventional trap

4.3.1 Validation of two-choice experiments for *G. f. fuscipes*

Catches of a biconical and a pyramidal trap in a multiple choice situation were compared to determine if such design could provide an unbiased information on colour and shape preferences by *G. f. fuscipes*; their performance is already known to be very similar from conventional latin square-designed experiments.

There was no significant difference in catches of both sexes, and of adults and tenerals from the standard (Challier-Laveissière) biconical trap and the standard blue/black pyramidal traps (Table 30). All categories showed a catch index close to 1.0; except for female tenerals which had a catch index of 1.88 in favour of the pyramidal trap as compared to the standard biconical trap. It is suggested that multiple choice experiments with *G. f. fuscipes* can provide a reliable information.

Table 30: Catches in standard biconical and in standard pyramidal traps (n = 11) set on a continuous lakeshore vegetation with an open background.(K=Kolmogorov-Smirnov test)

sex, status, total	mean # flies caught (±SE)		T score probability
	Biconical	Pyramidal	(±SE)
male	5.7 ± 1.31	5.6 ± 1.66	0.99 K
male teneral	0.4 ± 0.20	0.6 ± 0.45	0.36
female	16.8 ± 2.41	17.3 ± 3.62	0.90
female teneral	0.7 ± 0.32	1.3 ± 0.36	0.22
Total	23.7 ± 3.26	25.0 ± 5.36	0.84

4.3.2 Comparison of blue/black standard pyramidal or biconical traps with some blue/red candidates

Since previous experiments (section 4.1.1) showed that purple red may be useful in attracting *G. f. fuscipes,* traps with various designs (red inside instead of black, red outside alternating with blue, pyramidal shape, biconical shape) were compared with the standard pyramidal and biconical traps. Whenever the red colour was used outside the biconical trap, the usual black cloth was kept inside.

4.3.2.1 Turkey Red 721/3 (Red1): i. pyramidal shape

Comparisons between a pyramidal trap with blue and Turkey red and the standard pyramidal trap on a discontinous lakeshore vegetation with a bushy background (Table 31) gave a considerable increase of the catch of males (catch index = 2.1) and females (2.42) but the variance was too high. There was, however, no significant increase of the catch as compared to a standard pyramidal trap. When such blue/red pyramidal traps were tried at other sites which differed by the type of lakeshore vegetation (continuous or discontinuous) and background (bushy, not bushy, corridor present or absent) and fly abundance, the catch index was very low, in the range 0.38-0.98 for males and 0.54-0.74 for females. This suggested that such a combination was not efficient (appendix. 9-11)

ii. Turkey Red 721/3 (Red1): Biconical shape

A biconical trap with 50% red and 50% blue alternating on each half of the trap caught slightly less flies than the standard biconical trap (index 0.88 for males and 0.89 for females) (Table 32).

Table 31: Catches in standard pyramidal blue/black and in a pyramidal blue/red-Turkey red- (n = 7) set on a discontinuous lakeshore vegetation with a bushy background

sex and total	mean # flies caught (±SE)		Kolmogorov score prob.
	Biconical	Pyramidal	
male	3.0 ± 0.37	6.3 ± 3.27	0.80
female	7.2 ± 1.50	17.6 ± 5.93	0.39
total	10.2 ± 1.47	24.0 ± 8.41	0.39

Table 32: Catches in a standard biconical trap and in a biconical with blue and red (Turkey red) on the outer side (n = 7) set on a linear lakeshore vegetation site.

sex or total	mean # flies caught (±SE)		T-test score
	standard	modified biconical	prob.
male	13.1 ± 6.43	11.5 ± 6.53	0.88
female	5.7 ± 2.13	5.1 ± 1.56	0.89
total	18.8 ± 8.43	16.7 ± 7.94	0.89

4.2.2.2 Doge Purple 732/1 (Red2)

i. biconical shape

A biconical trap with 50% red and 50% blue alternating on each outer side caught less males (range of index 0.32-0.55) than a standard biconical trap. Such a trap caught significantly ($P < 0.05$) less females than the standard (Table 33; appendix 12). When red colour was used inside the trap (to replace the usual black) the catch index of males varied from 0.62-1.10 with a high variance in both cases (appendix. 13-14).

4.3.2.2 Doge Purple 732/1 (red2)

ii. pyramidal shape

A pyramidal trap on which the usual black was substituted by this red colour caught highly significantly less ($P < 0.01$) flies of both sexes than a standard pyramidal trap (Table 34). At some types of sites, its catch index was as low as 0.49 ($P < 0.25$) for males and 0.56 for the females ($P < 0.20$) (appendix 15). Results show that this variant of red is not a good candidate as compared to the usual black colour in combination with royal blue.

4.3.2.3 Peoney Purple 729/1 (Red3)

i. Biconical shape

Table 33: Catches in standard biconical trap and in biconical with blue and red (Doge purple) on the outer side (n= 5) set on a linear lakeshore vegetation site

sex or total	mean # flies caught (±SE)		T-test
	standard	modified biconical	prob.
male	9.2 ± 3.54	3.0 ± 0.70	P = 0.69k
female	5.2 ± 0.85	2.0 ± 0.70	P = 0.02*
total	14.5 ± 4.29	5.0 ± 0.00	P = 0.06

Table 34: Catches in standard pyramidal blue/black (n = 6) and pyramidal blue/red - Doge purple- (n = 7) set on a continuous linear lakeshore vegetation with an open background.

sex or total	mean # flies caught (±SE)		T-test prob.
	standard pyramidal	modified pyramidal	
male	4.5 ± 0.76	1.5 ± 0.57	0.0097**
female	6.8 ± 0.94	2.5 ± 0.68	0.0034**
total	11.3 ± 1.22	4.1 ± 1.18	0.0015**

Table 39: ANOVA for comparison of catches of *G. f. fuscipes* from a blue/black standard biconical trap and a new blue/red biconical trap (n=25 replicates; Rusinga/Island, Western Kenya; log10 transformation)

Source	df	SS	MS	F	P>F
Day (males)	1	0.013	0.013	0.23	0.634
site (males	9	6.213	0.690	11.91	0.0001**
trap (males)	1	0.025	0.025	0.44	0.513
day (females	1	0.034	0.034	0.49	0.489
site (females)	9	2.036	0.226	3.18	0.005**
trap (females)	1	0.419	0.419	5.89	0.020
day (total)	1	0.001	0.001	0.02	0.878
site (total)	9	4.154	0.461	5.72	0.0001**
trap (total)	1	0.412	0.412	5.12	0.029*

Table 40: Catch index of an unbaited blue/red (peony purple) biconical trap under various fly abundance levels. The abundance is given as the catch per day in the control trap (unbaited blue/black biconical trap). Abundance is defined in 3 classes: high > 20 flies; moderate 10-19 flies; low 0-10 flies/day. Letters apply for decision within one sex. * for P = 0.03; Kruskal-Wallis chsq. approximation. Decision from comparison of catches is done within density class and sex as shown by letters.

sex	density class	mean index	n	stderr	cv
M	high	0.82	5	0.173	47.0
M	moderate	0.67	5	0.168	55.7
M	low	1.54	15	0.329	76.9
F	high	0.59	3	0.315	92.5
F	moderate	1.03	4	0.280	54.9
F	low	2.92*	18	0.610	86.8

A biconical trap with 50% red and 50% royal blue alternating on the outer sides, caught less males (catch index 0.56-0.65) and less females (catch index 0.60-0.87). A biconical trap with this red inside, caught 1.28 times more males and 1.76 times more females at a site with moderate tsetse population (Table 35). At another site with a denser population, the indices were 1.08 for males and 1.20 for the females (appendix 16). In both cases, the variances were close to or lower than those of the catches in the standard trap. These results confirmed the observations on electric screens, where this same colour performed significantly better than black and blue for landing.

The principle that a colour with a high rate of milling around should be put outside (long-range attraction and a colour with high landing rate inside to stimulate entering the trap) was confirmed (appendix 17-18). It was also shown that red colours with different brightness performed differently (Fig. 6). A monoscreen shape had a poor performance (Table 36).

Further trials with this biconical trap with a peony purple target were conducted in a 2x2 design, alternating every day the two traps (control and treatment) in different biotope types. The catch of males in the blue/red trap was similar (index 1.21; $P = 0.41$) to that of the standard, but the catch of females was significantly increased (index = 1.63; $P = 0.02$); the total catch was also significantly (index = 1.43; $P = 0.02$) improved (Table 37). In 16% of cases, the blue/red trap caught less flies, the index dropping as low as 0.52-0.58; although the difference was not statistically significant in these cases. When all the replicates were pooled (including the 16%), the ANOVA model was valid for both sexes and for the total catch ($P < 0.01$). As a source

Table 35: Catches in standard biconical trap and in biconical with blue and (peony purple) red inside (n = 5) set on a discontinuous linear lakeshore vegetation with very bushy background

sex or total	mean # flies caught (±SE) standard	modified biconical	T-test prob.
male	7.8 ± 1.77	10.0 ± 1.58	0.38
female	6.0 ± 2.07	10.6 ± 1.07	0.08
total	13.8 ± 3.63	20.6 ± 1.98	0.13

Table 36: Catches in a monoscreen trap with a blue/red (peony purple) wing and in a standard blue/black biconical trap (n = 10)

trap	males	females	total
monoscreen	2.0 ± 0.61**	1.3 ± 0.47**	3.3 ± 0.97**
biconical	6.3 ± 0.81	4.0 ± 0.89	10.3 ± 1.52

Table 37: Catches of *G. f. fuscipes* in a blue/red (peony purple) biconical trap compared to a standard. blue/black biconical trap on Rusinga Island, western Kenya; Results from sites where responses were similar are pooled. Males and females and total successively shown for each case (means of catches/day ± SE).

control	blue/red	n	prob.	catch index	case
14.5 ± 5.42	8.5 ± 4.05	4	0.44	0.58	decrease
25.0 ± 9.22	13.0 ± 5.19	4	0.40	0.52	
39.5 ±13.14	21.5 ± 8.56	4	0.44	0.54	
6.5 ± 1.60	7.9 ± 1.68	21	0.41	1.21	increase
6.6 ± 1.21	10.8 ± 1.41	21	0.003	1.63	
13.1 ± 2.61	18.8 ± 2.76	21	0.02	1.43	

Table 38: Validity of the model in the ANOVA for comparison of catches of *G. f. fuscipes* from a blue/black standard biconical trap and a new blue/red (peony purple) biconical trap (n = 25; Rusinga/Island, Western kenya; log10 transformation)

source	df	SS	MS	F	P>F
model (males)	11	6.25	0.56	9.81	0.0001**
model females)	11	2.49	0.22	3.18	0.0038**
model (total	11	4.56	0.41	5.15	0.0001**
Error (males)	38	2.20	0.05		
Error (females)	38	2.70	0.07		
Error (total)	38	3.06	0.08		
Corrected total	.	Rsq.	cv	RootMSE	Mean(log10
males	49	0.73	31.1	0.24	0.77
females	49	0.47	28.2	0.26	0.94
total	49	0.59	25.5	0.28	1.11

of variation, the trap type was significant for females (P = 0.02) and for the total catch (P=0.029) (tabs. 39-40). The four replicates (out of 25) in which the blue/red trap failed to increase the catch were characterized by higher abundance of flies (25.0 ± 9.22 flies/day) as compared to the rest (6.6 ± 1.21) (Table 41). Hence, the effect of fly abundance on trapping was further explored. Moreover, the ANOVA (Table 38) indicated that R-square was low for females ($r^2 = 0.47$), meaning that day, site and trap type account only for 47% for the catch of females. Which other factors affect the catch of female *G. f. fuscipes*? Are catches in baited traps as well influenced by the abundance of flies?

4.3.3 Responses to host smell-baits on a standard (blue/black) trap.

i) Cow urine at a changing age of storage

Zebu urine was tested at different ages of storage. The catch of a standard biconical trap baited with 0-1 week zebu urine was not significantly different from the control (Table 42). In most cases, its index was 0.57 for males, 0.98 for the females and 0.8 overall. Only in 25% of the replicates, it reached an index of 1.0 for males and 1.24 for females, which was not a significant increase (P = 0.76 and P = 0.77 respectively).

Table 41: Comparison of catches of *G. f. fuscipes* with a blue/black standard unbaited biconical trap or baited with 0-1 week old cow urine; sites with similar effects are pooled; numbers successively represent males, females, total catch.

	standard	baited	n	F-test Prob.	index	case
males	4.5 ± 1.45	2.6 ± 0.60	12	0.32	0.57	decrease
females	5.4 ± 0.49	5.3 ± 1.26	12	0.38	0.98	
total	10.0 ± 1.72	8.0 ± 1.80	12	0.20	0.80	
males	3.7 ± 1.25	3.7 ± 0.85	4	0.76	1.00	increase
females	8.2 ± 1.31	10.2 ± 3.06	4	0.77	1.24	
total	12.0 ± 2.27	14.0 ± 3.13	4	0.75	1.16	

Table 42: Catches of *G. f. fuscipes* in a standard biconical trap baited with acetone and cow urine 3-4 weeks) (unbaited trap as control) on low-abundance sites at Rusinga Island (means ± stderr; males, females, total are presented successively)

	control	baited trap	n	prob.	index
males	0.7 ± 0.49	1.1 ± 0.39	8	0.41	1.5
females	3.1 ± 1.12	3.1 ± 0.93	8	0.76	1.0
total	3.8 ± 1.49	4.2 ± 1.06	8	0.43	1.1

Table 43: Effect of cow urine (4-5 weeks old) and acetone on the catches of *G. f. fuscipes* in biconical trap; sites 1-5m close to the Victoria lakeshore (numbers successively represent means ± stderr for males, females and total catch; sites with similar effects pooled).

control	baited trap	n	prob.	index	Effect
0.4 ± 0.33	1.6 ± 0.41	12	0.01**	4.00	increase
2.2 ± 0.60	1.9 ± 0.49	12	0.17	0.90	
2.6 ± 0.78	3.5 ± 0.83	12	0.36	1.30	
4.2 ± 0.75	3.0 ± 0.91	4	0.30	0.70	decrease
8.0 ± 0.70	6.0 ± 1.00	4	0.17	0.75	
12.2 ± 1.25	9.0 ± 1.77	4	0.20	0.70	

Zebu urine which was 3-4 weeks old, in conjunction with acetone (dose: 14.2-23.8 g/day) led to an index of increase of 1.5 for males and no change for females (catch index 1.5 for males and 1.0 for females). These results were from experiments conducted at low abundance sites on Rusinga Island (Table 42). When the same experiment with acetone and 3-4 weeks old zebu urine was conducted at Kisui area with higher fly abundance, the index of males was increased 1.5 times ($P = 0.18$) and that of females 1.38 times ($P = 0.30$; mean catch = 23.3 flies/day; $n = 18$). However, the urine repelled flies in 50% of the trials. In the latter case the index was 0.86 ($P = 0.90$) for males and 0.90 for females ($P = 0.48$) at sites where the mean catch was high (30.4 flies/day) (appendix 19).

Zebu urine which was 4-5 weeks old, in conjunction with acetone, led to a significant increase of the catch of males (index = 4.0; $P = 0.01$; mean catch 2.6 flies/day), but not so for females. In 25% of these trials there was a considerable repellency (Table 44). Indices of catches from a standard biconical trap baited with 5-6 weeks old cow urine were classified by fly abundance and by sex (tabs. 45-46). The lowest indices were obtained for males and females (0.47; $P < 0.05$) at the highest fly abundance levels (> 20 flies/day); followed by sites with moderate abundance (10-19 flies/day) where the index of males was 0.72 and 1.25 for females. The highest indices occurred at sites with low abundance of tsetse (range of catch 0-10 flies/day). In the latter case, the catch indices reached, 1.70 for males and 2.32 for females respectively (significantly higher than the other indices; $P < 0.05$)

Table 44: Catch index of a biconical trap baited with zebu urine (5 weeks) and acetone under various fly abundances. Abundance is defined as the catch/day in the control trap (unbaited Challier-Laveissière blue/black biconical trap). Abundance is categorized in 3 classes: 1) > 20 flies 2) 10-19 flies 3) 0-9 flies/day; * for $P < 0.05$ Kruskal-Wallis chsq approximation. Comparison of catches was done within abundance class and sex .

sex	density class	mean index	n	SE	cv
M	high	0.38*	4	0.099	51.4
M	moderate	0.72	6	0.156	52.5
M	low	1.70*	7	0.493	70.7
F	high	0.47*	4	0.074	31.0
F	moderate	1.25	6	0.290	56.6
F	low	2.32*	7	0.628	71.6

Table 45: Overall variation of the catch index of a blue/black biconical trap baited with zebu urine (5 weeks) and acetone under changing fly density. The abundance is given as the catch per 24 h in the control trap (unbaited blue/black biconical trap). abundance is defined in 3 classes: i) >20 flies ii) 10-19 flies iii) 0-10 flies/day.

abundance class	n	mean index	SE	cv
high	4	0.44 b	0.053	23.9
moderate	6	0.95 ab	0.156	39.8
low	7	2.08 a	0.549	69.8

Means followed by the same letter are not signif. different ($P = 0.05$)

A negative response occurrred again at higher abundance of flies (14.2 ± 2.77 flies caught per 24 h) as compared to lower (8.1 ± 1.47 flies/day) abundance where the catch was increased. It is suggested that 5-6 weeks old cow urine was best for females and at 4-5 weeks old urine for male *G. f. fuscipes*.

7-8 weeks old cow urine was still attractive but responses were erratic (Table 47). The index of males was 1.59 ($P = 0.41$) and 1.93 for females ($P = 0.06$) and 1.82 ($P = 0.10$) overall as compared to an unbaited standard biconical trap. However, in 50% cases, the index was 0.48 ($P = 0.24$) for males and 0.77 for females ($P = 0.67$).

Table 46: Effect of 7-8 weeks old cow urine on the catch of a blue/black standard biconical trap to *G. f. fuscipes* at sites 1-5 m close to the Victoria lakeshore; unbaited blue/black as a control; numbers successively represent males, females and total catch; sites with similar effects pooled.

	control	baited trap	n	prob.	index	Effect
males	5.2 ± 1.44	2.5 ± 0.52	7	0.24	0.50	increase
females	9.0 ± 2.69	7.0 ± 1.85	7	0.67	0.78	
total	14.2 ± 2.77	9.5 ± 1.95	7	0.21	0.70	
males	2.2 ± 0.96	3.5 ± 1.25	7	0.41	1.60	decrease
females	5.8 ± 1.10	11.2 ± 1.94	7	0.06	1.90	
total	8.1 ± 1.47	14.8 ± 2.24	7	0.10	1.80	

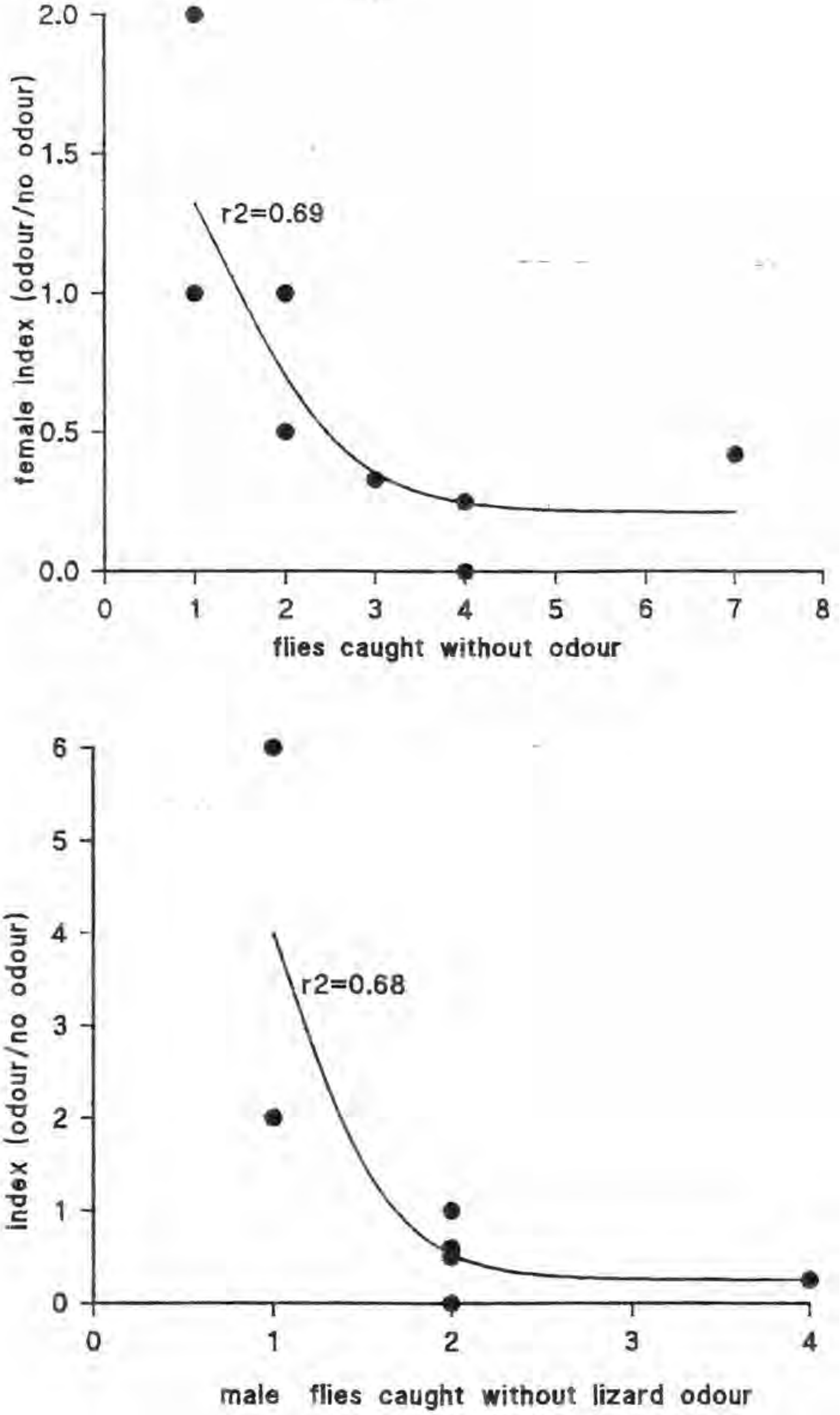


Figure 25: Catch from a standard biconical trap when whole body odour of a Nile monitor was used as a bait for (i) females and (ii) males. Data from 11 sessions of 30 min.

ii) Responses of *G. f. fuscipes* to whole body smells of Nile monitor lizards

The importance of *V. niloticus* as a host for *G. f. fuscipes* has been demonstrated through blood meals analyses (Weitz, 1963; Molloo, 1993 and Mohamed-Ahmed and Odulaja, 1997). Hence the effect of whole body volatiles of *V. niloticus* was evaluated as a bait. In fact, the responses to monitor urine, anemotactic responses, and body zone preferences, rate of feeding, co-occurence in the habitat have been reported in previous sections of this thesis. This part of the study summarizes results of experiments in which catches with whole body odour from the monitor lizard were investigated.

i) Validation of the method

No significant effect of air blown alone was detected (Table 48). Paired t-test was used to test the difference between catches with fan on (YES sessions) and with fan off (NO).

Some environmental factors which might effect the behaviour of the fly and the catch index (ratio catch YES/catch NO) were also taken into consideration: these included solar illumination and time of day. The effect of fly abundance as an intrinsic factor is illustrated by Fig. 25.

ii) Conclusion

The catch index was an inverse function of fly abundance at the sites (Fig. 25). Results of this experiment show that *Glossina f. fuscipes* was not indifferent to whole body odour of the monitor lizard, *V. n. niloticus* (Table 49). What was less evident is whether there was attractancy or repellency. A strong factor which should be taken into account to solve this paradox (both for males and females) is fly abundance.

Table 47: Validation of the method: sessions (4 ON; 4 OFF) with the PVC tube containing no lizard were run to check if air pressure alone might have any significant effect on the catches

session	sex	number of flies caught				T-value	Prob.
fan on	M	0	2	3	0	-1.039	0.37
fan off	M	4	1	2	4		
fan on	F	1	0	0	0	-1.73	0.18
fan off	F	1	0	1	1		

Table 48: Catches of a biconical trap when a monitor lizard in the PVC tube was ventilated or not; the results of the paired t-test are also given.

session	sex or total	n	number of flies caught											T-value	P
fan on	M	11	2	1	6	1	1	1	0	2	0	0	1	-0.28	0.77
fan off	M		2	4	1	2	2	2	2	1	1	0	0		
fan on	F	11	2	1	1	0	1	0	2	1	3	1	0	-2.58	0.02
fan off	F		2	1	2	4	1	0	1	3	7	4	2		
fan on	total	11	4	2	7	1	2	1	2	3	3	1	1	-2.04	0.06
fan off	total		4	5	3	6	3	2	3	4	8	4	2		

Table 49: Mean catch index of *G.f.fuscipes* (lizard odour/no odour) in the presence or absence of lizard odour at different light regimes and time of day.

range of light (µE/m^2/s)	**500-2000**	**>2000**	
Males	1.37 (166.5)	0.25 (141.4)	
Females	0.65 (63.3)	0.75 (145.2)	
Total	0.82 (96.3)	0.47 (35.8)	
range of time (hr)	**0900-1100**	**1100-1300**	**1300-1500**
Males	1.25 (84.8)	0.45 (82.4)	3.00 (141.4)
Females	0.16 (141.0)	0.73 (49.9)	0.83 (124.8)
Total	0.45 (89.9)	0.53 (50.4)	1.16 (86.8)

Even if a higher attraction had been observed when solar illumination was between 1,500-2,000 μE/S/m^2 (PAR measurement), and between 0900-1100 h and between 1300-1430 h for males, none of these two factors explain at all the responses of females (Table 50). In fact, it was shown previously that catch indices of females are more sensitive to fly abundance.

4.3.4 Responses to odour baits on the blue/red (peoney purple) trap

4. 3. 4. 1 cow urine smells at various ages of storage

A blue/red biconical trap baited with 0-1 week old zebu urine caught significantly less males (index = 0.50; P = 0.01) and slightly less females (index = 0.88; P = 0.48) than a standard biconical trap (Table 50). The total catch was significantly lower (index = 0.72; P = 0.04; mean catch = 12.0 flies/day). However, at sites with low fly abundance (6.2 flies/day ; 25% of the cases), the baited blue/red trap had a significant increase of females (index = 1.90; P = 0.02) and 1.75 for males (though, not significant). The total catch was also significantly higher (index = 1.80; P = 0.03).

When the blue/red biconical trap was baited with 2-3 weeks old cow urine(Table 52), three cases emerged: at sites with high fly abundance (25.1 flies/day) there was a slight repellency for males (index = 0.62; P = 0.51) and a significant repellency for females (index=0.34; P = 0.01). At sites with moderate abundance (8.1 flies/ day), there was a highly significant attraction (index = 2.63; P= 0.01) for males and a slight decrease of females (index = 0.98; P = 0.80). At sites with low abundance of flies (3.9 flies/ 24 h) there was a considerable increase in the catch of males (index = 2.87; P = 0.10) and a highly significant increase in the catch of females (index = 2.86; P = 0.001).

Table 50: Comparison of catches of *G. f. fuscipes* from a blue/red biconical trap baited with 0-1 week old cow urine as compared to the unbaited standard biconical trap; (sites with similar effects are pooled. K = Kolmogorov-Smirnov test used.

	n	control	baited trap	prob.	index	Effect
males	12	5.0 ± 1.03	2.5 ± 0.50	0.01	0.5	decrease
females	12	7.0 ± 1.41	6.2 ± 1.09	0.48	0.9	
total	12	12.0 ± 2.11	8.7 ± 1.47	0.04	0.7	
males	4	2.2 ± 0.62	4.2 ± 0.94	0.02	1.9	increase
females	4	4.0 ± 0.70	7.0 ± 2.12	0.18	1.7	
total	4	6.2 ± 1.03	11.2 ± 1.60	0.03 K	1.8	

Table 51: Catches of *G. f. fuscipes* with a blue/red biconical trap baited with 2-3 weeks old cow urine as compared to the unbaited standard biconical (one to three sites pooled).

	n	unbaited blue/red control	baited blue/red trap	prob.	index	Effect
males	9	10.5 ± 4.02	6.3 ± 1.95	0.55	0.6	decrease
females	9	14.6 ± 5.18	5.1 ± 1.53	0.08	0.3	
total	9	25.1 ± 8.97	11.4 ± 3.04	0.17	0.4	
males	17	1.6 ± 0.38	3.0 ± 0.48	0.08	1.9	increase
females	17	7.0 ± 1.56	7.8 ± 1.13	0.32	1.1	
total	17	8.6 ± 1.73	10.8 ± 1.11	0.05	1.2	

Table 52: Catches of *G. f. fuscipes* at Kisui area with a blue/red biconical trap baited with 3-4 weeks old cow urine as compared to the unbaited standard biconical trap; sites with similar effects pooled.

	n	control	blue/red trap	prob.	index	Effect
males	9	10.1 ± 3.57	6.3 ± 1.95	0.51	0.6	decrease
females	9	15.0 ± 4.58	5.1 ± 1.53	0.05	0.3	
total	9	25.1 ± 7.91	11.4 ± 3.04	0.13	0.4	
males	17	1.4 ± 0.24	3.1 ± 0.45	0.01	2.21	increase
females	17	6.2 ± 1.52	8.1 ± 1.17	0.13	1.3	
total	17	7.7 ± 1.52	11.2 ± 1.12	0.01	1.4	

With cow urine aged 3-4 weeks, the increase of the catch of females was highly significant (index 2.56; P = 0.01) at low abundance levels, but less evident for males (index = 1.52; P = 0.48) (Table 53). At levels of 8.1 flies/day, there was already a repellency effect (index = 0.86 for males; P = 0.97 and for females; P = 0.72). At high abundance (11.7 flies/day) (Table 54).

With cow urine aged 5-6 weeks, the blue/red biconical trap caught highly significantly less females (index = 0.37; P = 0.01) at moderate abundance (10.5 flies/day). The increase of the catch of males (index = 1.43) was not significant (Table 55). At low abundance (5.4 flies/day), the increase of the catch of females was highly significant (index = 2.0; P = 0.008) as well as the total catch (index = 1.85; P = 0.004). The increase of the catch of males was not significant (index = 1.55; P = 0.26). With urine aged 7-8 weeks, the blue/red trap caught an equal number of female flies and in overall (index = 1.03 and 1.09) as compared to the unbaited blue/red and no difference occurred in any category at all densities (Table 56).

It is suggested that the attractiveness of zebu urine was less consistent at 7-8 weeks. The optimum effect of zebu urine on a blue/red trap was obtained with urine

Table 53: Catches of *G. f. fuscipes* with a blue/red biconical trap baited with acetone and cow urine (3-4 weeks) (standard biconical trap as control) at low-abundance sites at Rusinga Island.

	control	blue/red trap	n	Prob.	index
males	1.5 ± 0.64	2.5 ± 1.04	4	0.56	1.6
females	4.2 ± 1.49	6.5 ± 3.20	4	0.91	1.5
total	5.7 ± 1.88	9.0 ± 4.14	4	0.96	1.6

Table 54: Catches of *G. f. fuscipes* with a blue/red biconical trap baited with 4-5 weeks old cow urine and acetone as compared to the unbaited standard biconical; sites with similar effects pooled.

	n	control	blue/red trap	prob.	index	Effect
males	4	0.7 ± 0.47	1.0 ± 0.00	0.45	1.4	decrease
females	4	3.2 ± 0.62	2.2 ± 0.47	0.25	0.7	
total	4	4.0 ± 0.91	3.2 ± 0.47	0.54	0.8	
males	4	3.7 ± 1.65	2.7 ± 0.85	0.78	0.7	increase
females	4	6.2 ± 1.97	10.0 ± 2.85	0.16	1.6	
total	4	10.0 ± 2.85	12.7 ± 1.31	0.37	1.3	

Table 55: Catches of *G. f.fuscipes* in a blue/red biconical trap baited with 5-6 weeks old cow urine as compared to the unbaited standard biconical trap. Sites with similar effects pooled.

	n	control	blue/red trap	prob.	index	Effect
males	8	3.2 ± 0.92	4.6 ± 1.65	0.610	1.4	decrease
females	8	7.2 ± 1.62	2.7 ± 0.70	0.010**	0.4	
total	8	10.5 ± 2.43	7.3 ± 2.04	0.230	0.7	
males	12	2.0 ± 0.57	3.1 ± 0.79	0.260	1.5	increase
females	12	3.4 ± 0.77	6.8 ± 1.05	0.008**	2.0	
total	12	5.4 ± 1.12	10.0 ± 1.23	0.004**	1.8	

Table 56: Catches of *G. f. fuscipes* in a blue/red biconical trap baited with 7-8 weeks old cow urine as compared to the unbaited blue/red biconical trap; sites with similar effects pooled.

	n	control	blue/red trap	prob.	index	Effect
males	4	3.0 ± 2.67	3.5 ± 1.93	0.61	1.2	decrease
females	4	5.0 ± 1.29	2.7 ± 1.03	0.21	0.5	
total	4	8.0 ± 3.71	6.2 ± 2.56	0.64	0.8	
males	12	4.5 ± 0.86	5.7 ± 1.03	0.63	1.3	increase
females	12	13.1 ± 2.04	13.6 ± 1.69	0.75	1.0	
total	12	17.7 ± 2.75	19.4 ± 2.49	0.56	1.1	

stored 2-3 weeks, at moderate abundance of flies (< 10 flies /day) for males and only at low abundance for females (< 7 flies/day).

A blue/red biconical trap baited with 2-3 weeks old urine caught ca. three times more flies than a standard biconical trap and ca. two times more than a standard biconical trap baited with cow urine (3 weeks) and acetone (index 1.50 for the males and 1.38 for the females). The importance of baiting a blue/red trap was not evident for female flies (index of an unbaited blue/red as compared to the standard blue/black is 2.92 at low densities with 0-10 flies/day; $P < 0.05$). But there is a benefit of baiting for males (index = 2.87; $P = 0.10$) as opposed to 1.54 for an unbaited blue/red trap.

It seems that there is a resistance to increase the catch index above 3.0. Indices of males and females just reached 2.8. It could be an attribute of the 'anti-swarming behaviour' of *G. f. fuscipes*. Otherwise, zebu urine at the optimum age of attractiveness (olfactory bait) could have acted in synergy with the colour effect (visual bait). There is also need to conduct further investigations on the effect of fly abundance on the catch index.

4.3.3.2 Catches with blue/red biconical traps baited with monitor lizard urine

Fresh monitor lizard urine absorbed in a sponge was placed inside the blue/red biconical trap to avoid rapid drying. The catches of such a baited blue/red trap were compared to an unbaited biconical trap (tabs. 57-59). The sources of variation in this comparison are listed in the Anova (Table 58).

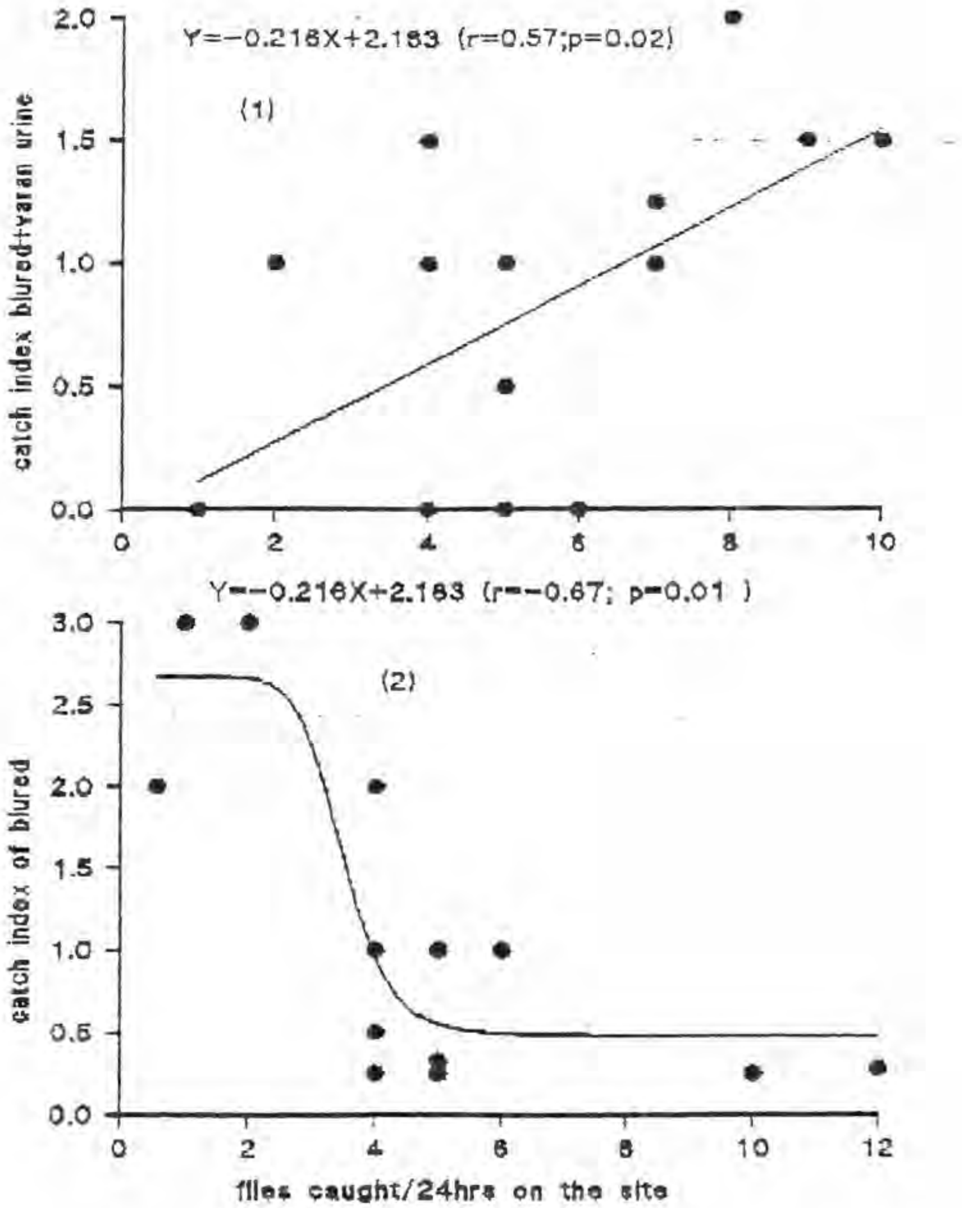


Figure 26: Catch index when the blue/red biconical trap was baited with fresh monitor lizard urine; standard biconical trap as a control ; (i) males (ii) females.

Table 57: Catches of *G. f. fuscipes* in a blue/red biconical trap baited with fresh monitor lizard urine (dispensed in a sponge); the unbaited standard biconical trap as a control; sites with similar effects pooled.

	n	control	blue/red trap	prob.	index	Effect
males	10	2.4 ± 0.45	1.5 ± 0.45	0.11	0.60	decrease
females	10	3.7 ± 0.65	2.4 ± 0.63	0.12	0.60	
total	10	6.1 ± 0.84	3.9 ± 1.00	0.05*	0.60	
males	12	3.0 ± 1.01	3.7 ± 1.18	0.62	1.20	increase
females	12	5.5 ± 1.41	7.1 ± 1.70	0.43	1.30	
total	12	8.5 ± 2.14	10.9 ± 2.78	0.49	1.30	

Table 58: Anova table for the comparison of the blue/red traps baited with fresh monitor urine vs standard biconical traps.

model	variable	df	F-value	Pr > F
	males	11	2.61	0.016
	females	11	3.44	0.0031
	total	11	3.81	0.0015
Source	variable	df	F-value	Pr > F
trap	males	1	0.13	0.716
site		7	3.83	0.0039
day		1	0.00	0.990
replicate		2	0.86	0.432
trap	females	1	0.02	0.895
site		7	5.01	0.0007
day		1	0.01	0.93
replicate		2	1.38	0.265
trap	total	1	0.08	0.77
site		7	5.67	0.0003
day		1	0.02	0.90
replicate		2	1.05	0.361

Table 59: Mean (± SE) catches of *G. f. fuscipes* in a blue/red biconical trap baited with fresh lizard urine. Unbaited standard biconical trap as a control.

	n	control	blue/red trap	index	Effect
males	5	5.8 ± 1.77	2.8 ± 0.80	0.48	decrease
females	5	9.0 ± 0.70	7.2 ± 2.31	0.80	
total	5	14.8 ± 2.05	10.0 ± 2.86	0.67	
males	15	1.7 ± 0.35	1.9 ± 0.52	1.10	increase
females	15	2.7 ± 0.46	3.6 ± 0.79	1.30	
total	15	4.5 ± 0.64	5.5 ± 1.28	1.22	

Table 60: Catches in a blue/red biconical trap where a stuffed monitor lizard is exposed jointly with cow urine

vegetation status	sex of fly	control	blue/red trap	n	index
clear	male	4.3 ± 1.20	6.6 ± 0.33	3	1.53
	female	9.6 ± 1.33	14.3 ± 0.66	3	1.48
bushy	male	3.3 ± 2.84	4.6 ± 1.20	3	1.39
	female	5.3 ± 2.40	9.6 ± 2.84	3	1.81
very bushy	male	1.3 ± 0.88	0.6 ± 0.33	3	0.49
	female	5.0 ± 2.64	3.3 ± 1.76	3	0.66

Results of the Anova show that, overall, there was no significant difference between catches from a blue/red trap baited with Nile monitor urine and those of an unbaited standard biconical trap. Fly abundance also affects the catch index of a blue/red trap baited with lizard urine (Fig. 26; tabs. 57-59). At sites with a high abundance (catch/day between 10-25) the catch index of males ranged from 0.33-0.57 and the index of females ranged from 0.25-1.4. At sites with low abundance of tsetse, the catch index of a blue/red biconical trap baited with fresh lizard urine was slightly higher than that of an unbaited standard biconical (index = 1.10 for males and 1.30 for females).

The relationship between abundance of flies and catch index for monitor lizard fresh urine bait is shown on Fig 26. The response of male flies to lizard urine was weaker than that of females. The index of males varied between 0.5-1.5 at low abundance sites (1-10 flies/ day). But the index of females varied between 2.0-3.0 in most cases at sites with low tsetse abundance. An inflection at ca. 5 flies/day was again observed; above that point, the catch index of females dropped as low as 0.25-0.33. The trends of the relationship catch index-fly abundance were opposite for males and females. While the catch index of males increased directly with the increase of fly abundance, female flies entered less in the trap when the abundance of flies increased. Both relationships were significant (P = 0.02 for males and P = 0.01 for females).

4.3.5 Further investigations on the influence of fly abundance on the catch index

The classical factor "site" in tsetse studies is a complex. Several experiments in this study have shown that abundance (catch/day in the control trap) is a very important element of this complex. Thus, it could be advantageous to substitute the complex factor "site" by its simpler component "abundance class (scores based on ranges like 1= 0-10 flies/day; 2 = 10-20; 3= >20 flies/day) for *G. f. fuscipes*.

4.3.5.1 Variation of the catch index of an unbaited blue/red trap

A blue/red biconical trap performed better than a standard biconical trap (Table 40). However, its performance was strongly and negatively influenced by the abundance of flies at trapping sites. Fig. 27 shows that at very low abundance 0-3 flies/day, the catch index was very high (4.0-10.0).

When abundance was 4-6 flies/day, the catch was still doubled in the blue/red biconical trap (unbaited). But a strong point of inflection occurred at the level of 7 flies/day, where the blue/red trap was just as good as the the standard biconical trap. According to this curve, moderate abundance will fall between 7-20 flies/day. At high abundance (> 20 flies/day) the catch index was very low (ca. 0.25).

That relationship is represented for females by the equation:

$Y = 1.07 + 14.65 \cdot 10^{(-0.67X)}$;$R^2 = 0.86$; df = 21; $P = 0.0001$.

Thus, the relationship between the catch index of females and the inverse of the abundance is a strong linear relation:

$Y = 1/X$; $Y = 7.429 * X + 0.419$; $r^2 = 0.87$; $P = 0.0001$.

The catch index of males varied between 1.4-3.8 at the lowest abundance levels (0-7 flies/day). The latter index was also highly significantly related to the abundance of flies at the sites:

$Y = 1/X$; $Y = 3.296 * X + 0.495$; $r^2 = 0.46$; $P = 0.002$.

The point of inflection of the curve was again at ca. 7 flies/day. It decreased at sites with high abundance, but remained close to 1.0 in the region of high abundance.

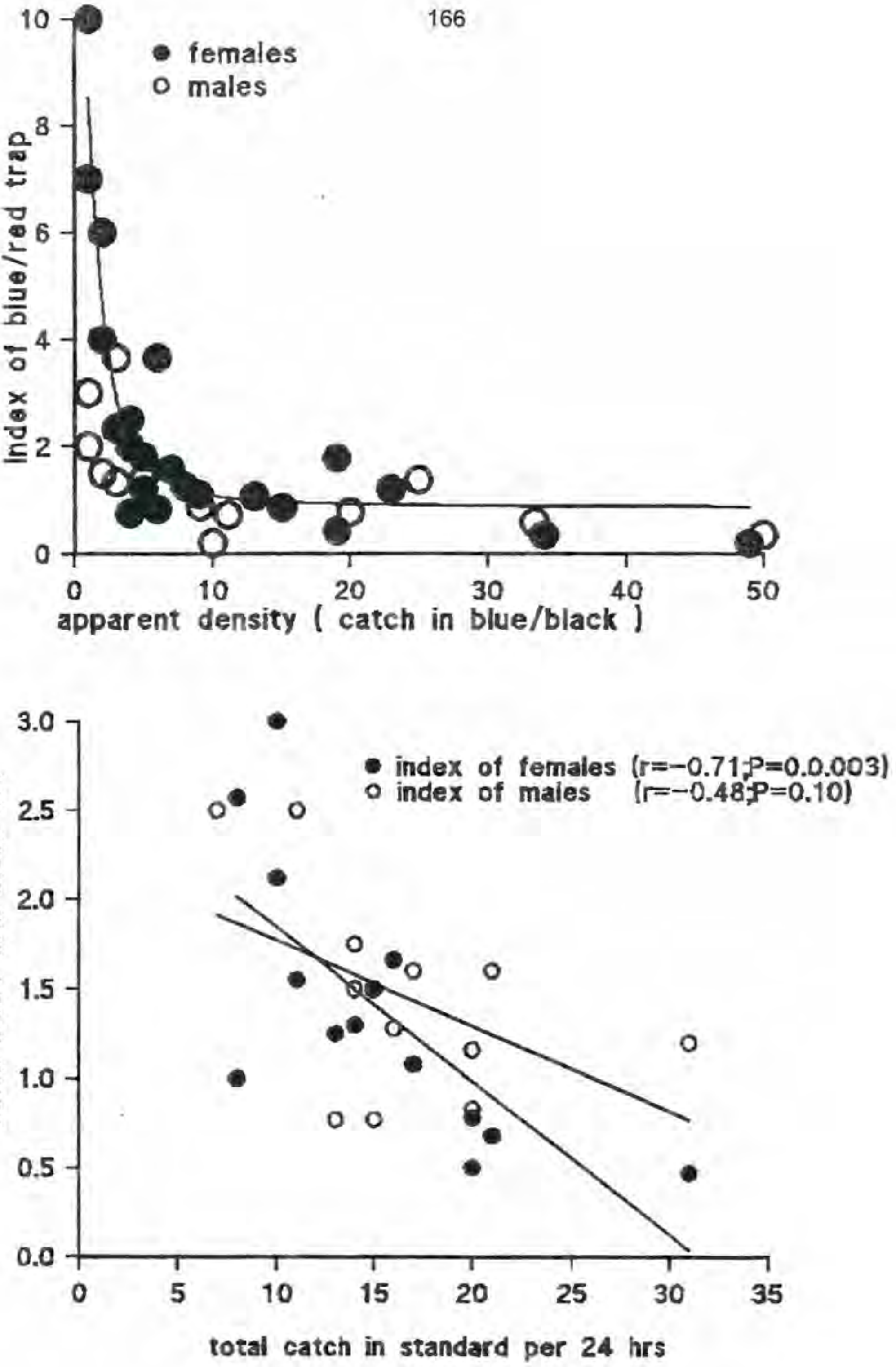


Figure 27: Relationship between catch index and fly abundance for a blue/red biconical trap with a (i) the usual white net upper cone or a (ii) a black net upper cone.

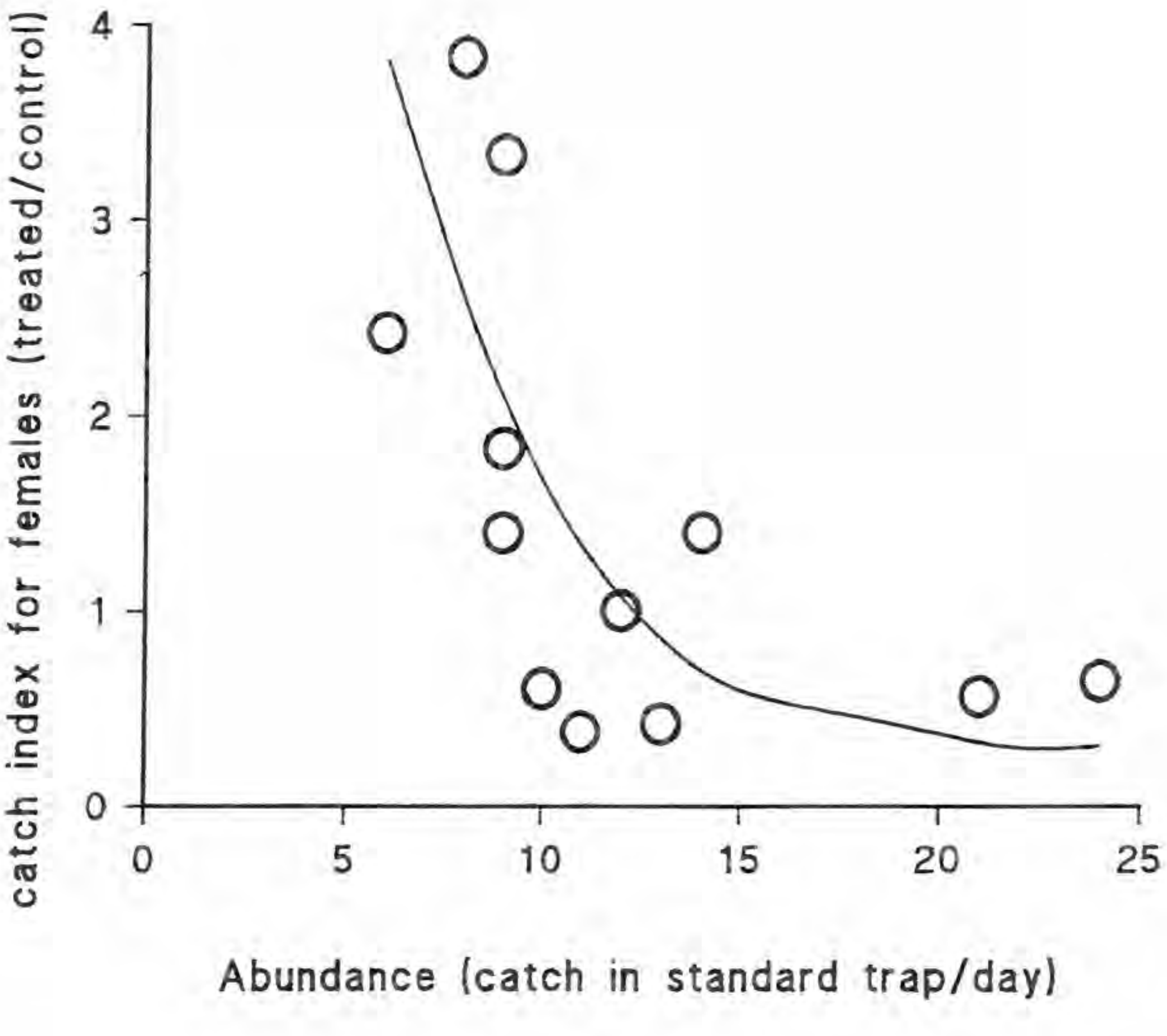


Figure 28: Variation of the catch index for *G. f. fuscipes* as a function of fly abundance when acetone and cow urine of 5 weeks were used as bait on the standard biconical trap

So, the catch of females increased faster at low abundance, but it also decreased relatively faster at high abundance as compared to the index of males. Perhaps, males are less sensitive than females to the "crowding-effect".

Originally, it was assumed that the important characteristic of the site which influences the catch is vegetation (visibility of the trap essentially). I compared catches in the blue/red biconical trap to catches in the standard biconical trap at sites which were all very bushy but carried sensibly different densities of tsetse.

At sites with catches above 15 flies/day in the control, catches from both traps were not significantly different for males and for females. At sites with lower abundance of flies (< 10 flies/day) the catch index of males was slightly increased and the catch of females ($P < 0.05$) was increased by 70% and similarly for the total catch. Fig. 30 shows that in this experiment the average catch index per replicate was doubled for males at low abundance levels and just close to 1.0 at high abundance ($rs = -0.56$; $P = 0.11$). The average catch index per replicate was 1.5 for females but as high as 2.8 at low abundance. The catch index was significantly (negatively) related to the abundance of flies ($rs = -0.75$; $P = 0.02$).

The same type of experiment was conducted at 10 sites. Vegetation at a given site was assumed not to change significantly during the experiment; but the abundance of flies per replicate was variable. With this higher sample size, it appeared clearly that at high tsetse abundance (> 15 flies/day), the catch index of the blue/red trap was significantly reduced down to half or lower. ($P < 0.05$). At moderate tsetse abundance (7-12 flies/day), the catch of females in the blue/red trap was similar to that in the standard biconical trap. At low abundance, the catch of the blue/red trap was significantly higher:

index of males = 1.41 - 0.015 mean catch; r = - 0.46;

index of females = 2.21 - 0.034 mean catch; r = - 0.79.

It is suggested that the characteristic of the site which mainly influences the catch index is not a physical factor (light, ease of movement, visibility) but abundance of flies. It is likely an intrinsic characteristic of *Glossina f. fuscipes*.

4.3.5.2 Variation of the catch index of biconical traps baited with cow urine

The variation of the catch index of biconical traps (standard and blue/red) at different levels of fermentation of cow urine is summarized in Table 61. Samples of zebu urine at 3 weeks of age were optimal for the catch of males in both trap types. For females, the optimum increase was obtained with cow urine of 5 weeks (Table 61). Thus, the total catch was more enhanced with cow urine of 5 weeks (at average room temperature conditions at Mbita, Western Kenya, circa 28 °C).

Table 61: Variation of the catch index of two types of biconical traps with the age of zebu urine used as bait. Only catches at low abundance sites i.e <10 flies/day were taken into account. * = significant change at P = 0.05, ** = significant change at P = 0.01, ac = acetone used in conjunction with cow urine.

weeks	blue/black standard		blue/red	
	males	females	males	females
0	0.57	0.98	1.90*	1.75
2	-	-	1.87	1.11
3	1.50	1.00	2.21**	1.30
4	1.50	1.38	-	-
4	4.0ac**	0.86ac*	1.42ac	0.68ac
5	1.70ac*	2.35ac*	1.55	2.0**
7	1.59	1.93	1.16	0.54

When acetone was used in conjunction with cow urine of 5 weeks, the catch of females was boosted 2.3 times on the standard biconical trap. Urine at 4 weeks likely repelled female flies when it was used in conjunction with acetone.

The dependence of the catch index on fly abundance was already demonstrated in this study, on an unbaited blue/red trap, on a baited blue/black trap and on a baited blue/red trap both with cow urine (Fig. 28) and monitor lizard smell. To verify if this density-dependence is really an intrinsic characteristic of *G. f. fuscipes* populations, I reanalyzed data from some authors. *G. pallidipes* had been caught in standard biconical traps baited with cow urine without following any trend of negative dependence. The exemple from Dransfield (1986) confirms instead that within abundance levels between 5-500 flies/day, the trap index increased very slightly as fly abundance increased:

index = 5.50 + 0.0052 * density; $r = 0.92$; $P < 0.01$.

Such that at an abundance level of 5 flies/day, the index was 5.43 and at 100 flies flies/day the index was 5.94. The trend remained true at huge catches of up to 500 flies/day.

Analysis on data from Gouteux (1995) on *G. f. fuscipes* in the Central African Republic ($r = -0.32$) and Mwangelwa (1990) on *G. f. fuscipes* on Rusinga Island in Kenya ($r = -0.49$) show that there is a tendency to negative relationship between the catch index and the density of *G. f. fuscipes* (Fig. 29). Larger samples could boost the statististical significance of that relationship.

The catch index of a standard biconical trap baited with 5 weeks old zebu urine in conjuction with acetone varied between 1.4-3.3 at sites with less than 10 flies/day;

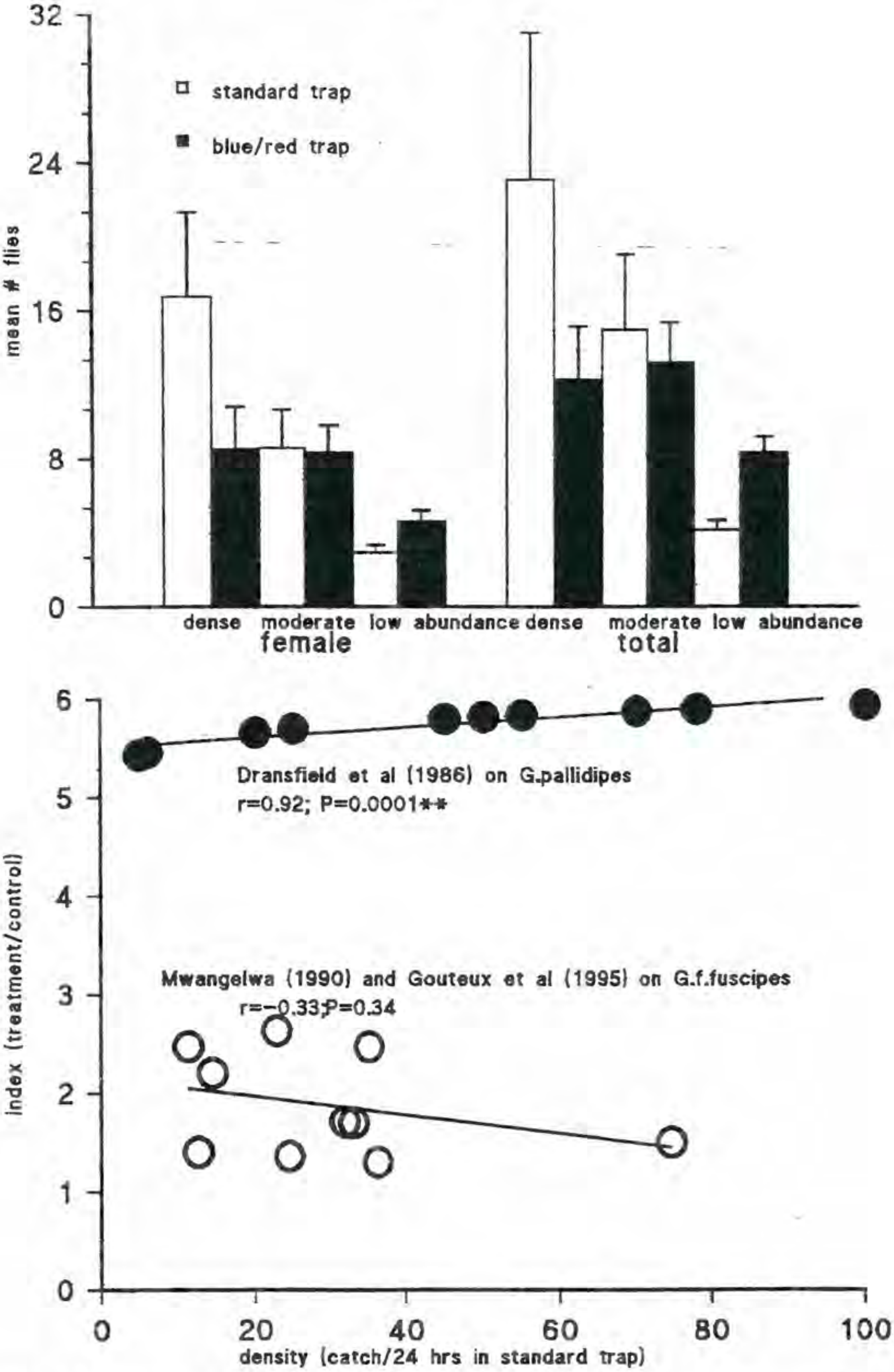


Figure 29: Influence of fly abundance on the catch index of (i) a blue/red biconical trap set at different sites and of (ii) a standard biconical trap baited with cow urine and tested in Kenya and in the Central African Republic by different scientists.

at higher abundance (10-60 flies/day) the catch index dropped to a range of 0.5-1.0) as compared to an unbaited standard biconical trap. The point of inflection of the curve occurred at 13 flies/day; where the catch dropped down to 0.5-0.25 or less. The index was only 0.25 at 60 flies /day. The equation (Fig. 28) for females is:

$$Y = 0.31+6.64x10^{(-0.14X)};\ R^2 = 0.46;\ df = 9; P< 0.001.$$

When a standard biconical trap was baited with whole body odours of the Nile monitor, the catch index of female flies followed this same inverse trend in relation with the number of females caught per session. When one fly was caught per session (sessions of 30 min.), the catch index reached 1-2; but at higher catches, the index dropped between 0.3-0.5. The same trend was observed for males where the few increases (index = 2.0-6.0) occurred with catches of 1 fly/30 min. With catches between 2-4 flies/30 min., the index was as low as 0.3-0.5 too. The relationship between the catch index and the inverse of the catch in the control was highly significant for females (r = 0.77; P = 0.008) and for the males (r = 0.79; P = 0.01). Results of these short trials of 30 min. suggested that the density-dependence of the catch index could be related with responses of *G. f. fuscipes* during encounters with its conspecifics on the trap.

4.3.5.3 Attempts to find the mechanism of the density dependence of the catch index

I tested the hypothesis of an "anti-swarming behaviour by avoiding conspecifics on the trap" by using the data from field binoculars observations (section 4.2) and also by attaching decoys (dead male flies stuck on the trap with a black thread).

It was assumed that the flies tend to disperse when they encounter conspecifics on a trap, and thus, enter less frequently.

Results from binocular observations (sessions of two hours; subsessions of 10 min.) showed that the rate at which *G. f. fuscipes* enters the cone of the standard pyramidal trap is inversely proportional to the number seen on the trap per subsession (Fig. 30):

Proportion entering = $- 0.12 X + 1.10$; $r = - 0.87$; $P < 0.0001$.

Above 2 flies/10 min, only 50-60% of the flies which approached the trap entered; but when only 1-2 flies approached the trap, they had a chance of up to 90 % to enter the trap.

The same occurred on the biconical trap (Fig. 30). When 1-2 flies alighted on the standard biconical trap, 45-90% entered the lower cone; when 3 or more flies alighted, only 20-55% of them entered the trap. The relationship between the proportion entering per 10 min. (subsession) and the number of flies landing per 10 min. was highly significant:

$$Y = - 0.12X + 1.03;\ r = - 0.76;\ P < 0.0001.$$

In another series of experiments, 5-10-15-20 decoys were stuck on standard biconical traps (Fig. 31). No significant relationship was found between the catch index of males and the number of decoys on the trap ($r = 0.22$; $T = -1.05$; $df = 22$; $P = 0.30$). But female flies entered more in the trap at lower numbers of decoys as opposed to higher numbers of decoys (10-20) (Fig. 31):

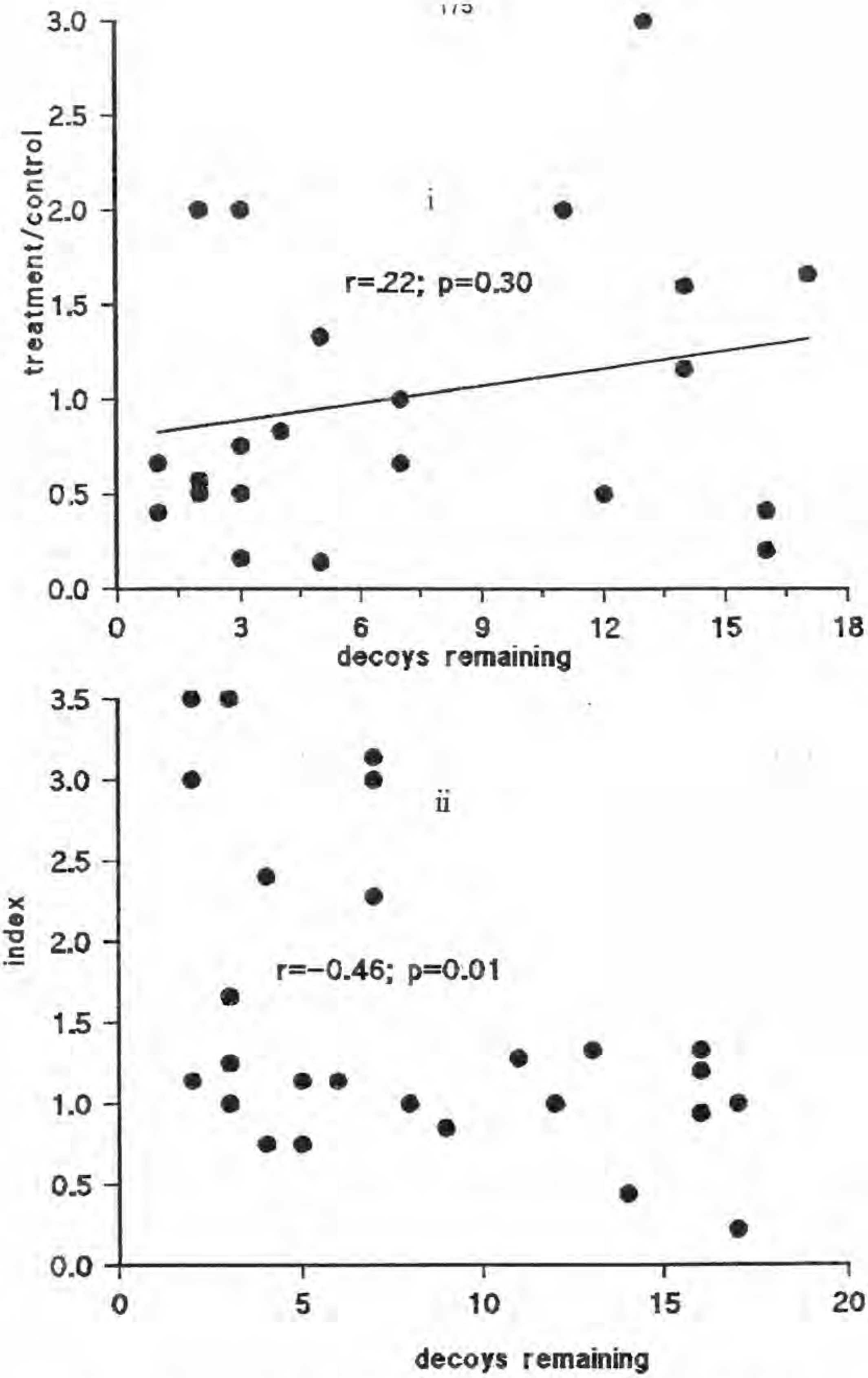


Figure 30. Catch index of a standard biconical trap (i) for males and (ii) females when various numbers of dead (male) flies was stuck on the lower cone.

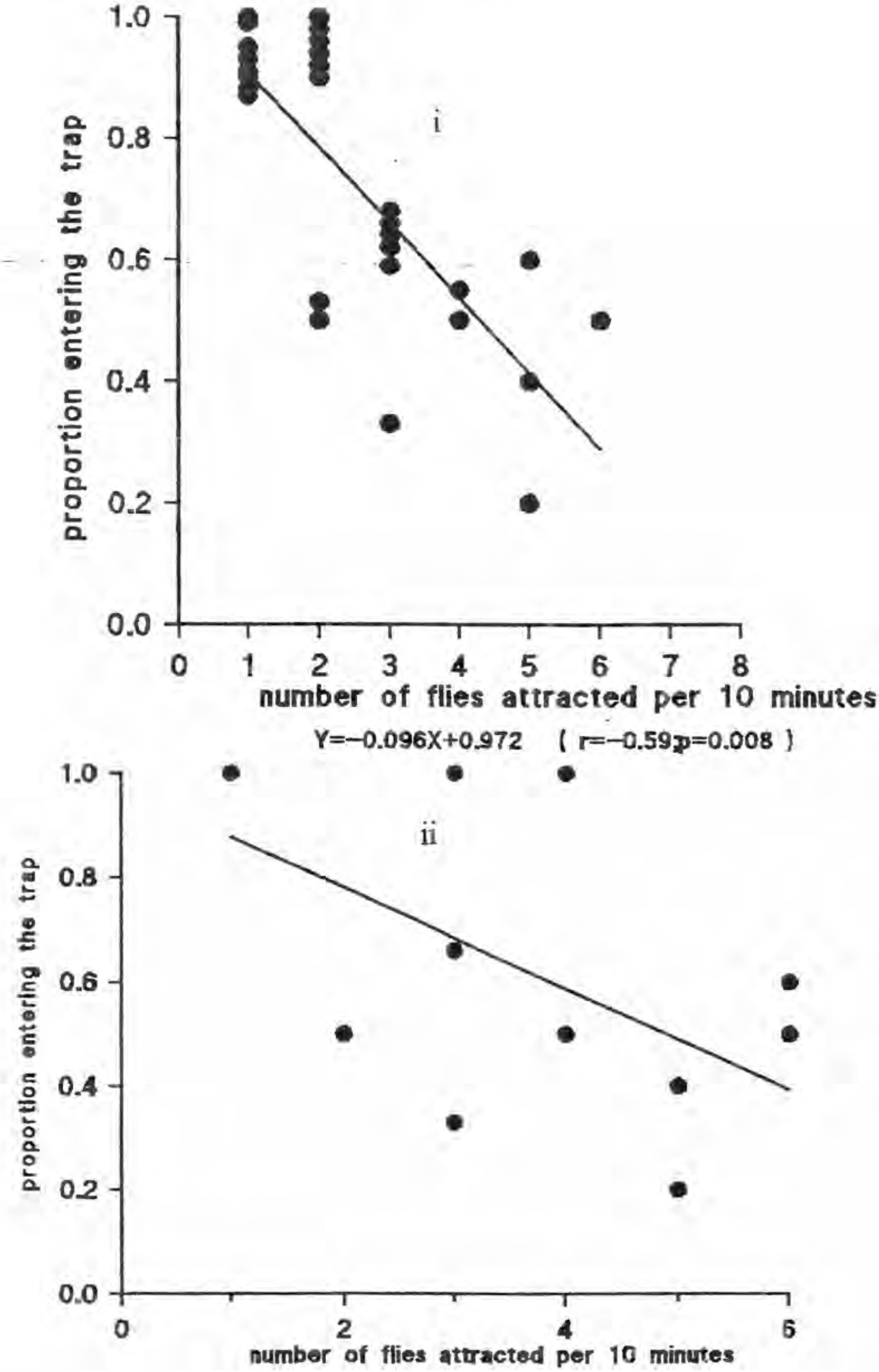


Figure 31: Relationship between the number of flies attracted to the standard pyramidal or (ii) biconical trap and the proportion entering into the trap.

$Y = 5.54 \cdot 10^{(-0.61X)} + 0.94$; $R^2 = 0.42$; df = 24; $P < 0.0001$; The determinism of effect of fly abundance on the catch index perhaps mainly relies on the appearance of the body of congeners because dead decoys elicited a clear response for females, which were usually more sensitive to this effect of abundance. Perhaps sound or movement or epideictic pheromones also play a role in "the anti-swarming behaviour" of *G. f. fuscipes*.

5. Discussion

5.1. Responses of *G.f.fuscipes* to colours

5.1.1. Responses to single-coloured targets

Results demonstrate for the first time a consistent predominance of red as compared to royal blue for eliciting the landing response of a tsetse fly. Red was also relatively more selective to females than to males as compared to the blue/black standard and the blue target, an additional advantage in trapping. The high attractiveness of royal blue as compared to black for landing is also unusual. Warnes (1991) showed that blue and black cloth are similarly attractive although the landing response is higher on a black cloth.

However, Gouteux and Noireau (1986) observed very few responses by *G.m.morsitans* and *G.austeni* to a blue target with a grey background. Against other backgrounds, *G.austeni* consistently preferred to land on blue targets, with about 2-3 times more landings on blue as compared to red targets. Green (1991) found that the relative landing frequency of *G.m.morsitans* and *G.austeni* on red and blue depended on both the background and the species.

Although a predominant landing on red is not common, a strong attractiveness to red has been demonstrated in some Diptera. Browne and Bennett (1980) showed clearly that both simuliids and tabanids have marked preferences for blue and red and black. Within Lepidopterans, Weseloh (1972) observed a strong preference of the gipsy moth to land on red, blue and black panels.

The number of *G.p.palpalis* attracted by blue was higher, but not significantly so, than those atracted by red, black and white (Green, 1988). Tests on

G.tachinoides, another riverine tsetse, showed that phthalogen blue is the most attractive colour and yellow the least, with black, red, violet and white intermediate (Green, 1990). Interestingly, the proceedings of the OAU tsetse conference held in Maputo (ISCTRC, 1997) show that the cloth fabric does not matter significantly in the attraction and landing of riverine tsetse, unlike savanna species.

Blue is widely considered as the most effective colour of material to use in the construction of tsetse traps and screens (Laveissière and Couret, 1981). However, that colour is not universally chosen. Dransfield et al (1982) insisted on the attractiveness of white, while yellow and green had been shown to be constantly unattractive (Allan *et al.*, 1987).

5.1.2. Responses to targets with combined colours

In this study, it was observed that none of the single colours, including blue and red could advantageously replace a blue/black target. For attraction, a blue/red target is the best combination (2.6 times more attractive than a conventional black target), followed by red/black (index = 1.98) and blue/black (index = 1.88). For the landing response, blue/red/black (index = 2.08) and blue/black (index = 1.88) are the best options to replace a conventional single black target. In fact, on a target, the objective is to cause the fly to land on the cloth portion or to collide with the flanking nets to pick up the insecticide.

In fact, the high sensitivity of tsetse flies to contrasts as a means to detect distant objects (Allan *et al.*, 1987) is known. In this respect, Muirhead-Thomson (1991) reported that colour combinations are useful for simple screens but not for flanked ones; in the absence of side-panels, blue-and-white targets were twice as good as all-blue targets for *G. pallidipes* and *G.m.morsitans*. But, colour combinations were no better than all-blue targets when mosquito netting panels were present.

In this regard, it seems that there might be a considerable difference between the savanna tsetse species (*G.m.morsitans* and *G.pallidipes*) and riverine tsetse. Contrast tests done by Green (1988) showed that blue and black is the best combination for *G.p.palpalis* even on a flanked screen, supporting the observations in this study on *G.f.fuscipes*. The higher attractiveness of red as compared to black is still reflected in a contrast test.

5.1.3 The spectral basis of the colour preference

The reflectance of experimental colours respectively in the blue wavebands (450-490 nm) and in the near infra-red range (760-1100 nm) allowed a satisfactory prediction of the intensity of the landing response and the attraction.

In the literature, variations and controversies arise about the effective wavelengths in the spectral responses of tsetse flies. Whereas Green and Cosens (1983) found a U-V sensitivity constantly higher than the sensitivity to the blue range, the reverse was found by Davis and Gooding (1983), both teams having investigated on *G.m.morsitans*. The former authors detected a third minor peak in the red range, but there was only a suggestion of such a peak by the latter team. Green and far red light gave no significant response above control levels (700 nm). Turner (1987) found positive correlations between trap performance and blue-green and u-v wavelengths for *G.pallidipes* in western Kenya. Green-yellow-orange wavelengths played a negative role on the catch.

While there is a consensus about the u-v peak of attractivity in savanna tsetse, the role of u-v is negative in riverine tsetse studied (Green, 1988 on *G.p.palpalis* and this study on *G.f.fuscipes*). This contrast is proved by the very poor performance of a blue-white diagonal combination in this study in the field, whereas it had elicited the maximum response in Zimbabwe on *G.m.morsitans* and *G.pallidipes* (Muirhead-Thomson, 1991).

Green (1988) showed that blue wavelengths contribute positively and violet, green-yellow, red negatively to trap performance for *G.p.palpalis*. U-V did not contribute to attraction and it did not repel the flies. Those findings suggest major differences between riverine tsetse and savanna tsetse.

The sensitivity to infra-red which is observed in this study had been seldom reported. Green and Cosens (1983) mentioned that an atypical feature of the wavelength preferences of tsetse is the greater attractiveness of red than green, a reversal of the usual situation in *Diptera*.

Five principal classes of insect photoreceptors are known, with sensitivity peaks in the ultra-violet (340-360 nm), violet to blue (420-470 nm), green (490-550 nm), red (610 nm) and infra-red (750 nm) regions of the light spectrum (Adil, 1995).

Recently, Gibson (1995) found that the malaria mosquito, *Anopheles gambiae* can detect near infra-red. She suspected that the mosquito eye may have specialized areas for detecting long wavelength light, which is difficult to pick up on an electro-retinogram, or even with single cell recording.

An early supporter of infra-red sensitivity is Callahan (1965). He noted that the visible region is, after all, only a very small portion of the electromagnetic spectrum. The insect's body is covered with tubes, hollow organs and lenses, such as the ocelli, which might well be resonators, waveguides, or filter type receptors for invisible radiation of longer wavelengths. Among the conditions he defined for optimum infra-red communication, I could mention that, *G.f.fuscipes* uses the Nile monitor as an important host; such a host generates heat (body temperature: 22-33°C), is covered with scales and has dark-patterned areas especially while basking. It basks on dry wood (the ambatch) which is a window for several far infrared (FIR) frequencies. The peak of activity of *G.f.fuscipes* occurs at a part of the day where relative humidity is minimum. At the eccritic temperature of the Nile monitor, the peak radiation could be circa 9.48µ, because the wavelength of peak radiation (λm), multiplied by the temperature (Ko) of the black body is equal to a constant or:

$\lambda m = 2897 / (273+32.5^{\circ}C)$ (Wien's displacement law, cfr Callahan, 1965).

All the range of body temperature at haul-out time (ca. 22 °C) will lie in the middle of the main IR window (7-14µ) , within which air is transparent to IR energy. The attenuation of the bands 9-10µ and 10-11µ is independent of weather changes. Reinouts van Haga and Mitchell (1975) found that tseste *G.m.morsitans* uses a secondary input from the temperature receptors on the tarsi, in addition to the primary input from receptors on the antennae.

Near infra-red light is strongly reflected by vegetation (Brightwell *et al.*, 1992) and net entropy flows from a lizard due to infra-red radiation, convection and evaporation of water can be in the ratios 1.0:1.4:0.02 and the entropy production of the lizard per gram can be 21 times higher than that of a mammal of 50kg (Aoki, 1988).

Special trends in the visual ecology of *G.f.fuscipes* could need an evolutionary consideration. This species belongs to the great central forest of Congo, although it has been capable of surviving in gallery forests in Congo Brazzaville, Uganda, Kenya, and in small isolated relict belts in South-west Ethiopia (Mulligan, 1970). Machado (1953) supposes that *G.palpalis* and *G.fuscipes* had a common ancestor. He believes that *G.f.fuscipes* is closest to the ancestral form (even than either of the two other subspecies of *G.fuscipes*). In fact, in the forest, as the gap fraction declines in the vegetation, the contribution of blue sky declines, and longer wavelengths dominate the irradiance (Endler, 1993).

The spectral choices in this study are related to field catches. Usually, much useful information is gained through behavioural methods and they show roughly the same peaks of sensitivity as electrophysiological ones, but they do not tell exactly what the relative heights of the peaks are (Burkhardt, 1977). In any case, many of the Dipterans are difficult to train, and, therefore, they display very clearly any natural preferences that they may have (Kalmus, 1948).

Apart from the effect of hue, the brightness of colours accounts also for the attraction of *G.f.fuscipes*. Strong brightness seemingly repels. Green (1984) observed that for 400 nm, low intensities were less attractive in *Musca domestica* and *G.m.morsitans* than the reference light ; but at 550 nm, low and moderate intensities were preferred, while the highest experimental intensity was less attractive than the reference. Elsewhere, *G.morsitans* performed no negative phototaxis. Also, an increase in the number of quanta reflected by a target in the region 530-560 nm stimulates its attractancy to female Hessian flies; but low intensities are favourable in the region 400-500 nm (Harris *et al.*, 1993).

However, an achromatic series of screens (black, white and grey) all attracted significantly fewer females of *G.p.palpalis* than did a royal blue screen, implying that attraction to blue depends on colour discrimination and not on intensity contrast alone (Green, 1988). Fukushi (1990) also observed that the blowfly, *Lucilia cuprina*, discriminates colours mainly by the hue, and that brightness perception plays a secondary role. The attractiveness of black, green and blue seems to rely considerably on the silhouette. The role of silhouette in the attraction of blood-suckers was mentioned by Gillies (1974).

5.2. Detailed behaviour around traps and light preferences

5.2.1 Detailed behaviour around traps

A number of inferences could be made from the results on detailed behaviour around biconical, Vavoua and pyramidal traps: the biconical trap leads in terms of catches due to a higher attractiveness to flies. The pyramidal trap may compensate its relatively weaker attractiveness by a higher rate of entries and its shorter duration of acts, a fly taking less time to enter the trap. The similarity of their catches (Mwangelwa, 1990; Mohamed-Ahmed and Odulaja, 1997) or the considerable success of the pyramidal (Gouteux and Le Gall, 1992) in trapping *G.f.fuscipes* could be explained that way.

Despite a strong similarity in shape and in behavioural repertoire with the pyramidal trap, the poorer performance of the Vavoua may have to do with a lower attractiveness to the flies. Interestingly, the rate of entries (biconical, 61.1%, pyramidal, 74.9% and Vavoua, 77.2%) of *G.f.fuscipes* is fairly high as compared to *G.pallidipes* as reported in the very few studies available. Owaga (1989) found that, of all the *G.pallidipes* seen to arrive at a standard biconical trap, 52.7% departed without attempting to enter the trap. Generally they alighted on the exterior surface, then took off. Even 17.5% of the total seen to arrive went in and out of the lower cone. Madubunyi (1992) also reported that most flies (87%) which alighted on the vertical target flew away and only 17% entered the trap cone.

Unlike the savanna tsetse, *G.pallidipes* investigated elsewhere, the riverine tsetse , *G.f.fuscipes* in this study could alight and take off from the external body of the trap but, once it reached the internal target it entered. In fact, Odulaja and Mohamed-Ahmed (1997) reported an efficiency of the biconical trap of up to 87% for *G. f. fuscipes*. Caution is needed about this high entry rate, because Späth (1994) found that only 18% of male and 9% of female *G. tachinoides* enter the standard biconical trap (respectively 30 and 18% for octenol-baited traps). There is more similarity between *G. fuscipes* and *G. tachinoides* in terms of choices of zones on the trap by landing flies; more than 90% of landing flies alight on the blue cone implying that logically any insecticide should be impregnated only on this part of the trap. Impregnation of the pyramidal and Vavoua (where less flies alight) with insecticides would yield relatively less success then the insecticide-impregnated biconical traps.

5.2.2. Light and sensitivity of traps

The ranges of light preferred by *G.f.fuscipes* had been estimated by Rogers (1977). He observed that there is an intermediate illumination at which the availability of male flies is at maximum. Both at lower illumination (belt of tall forests) and at high illumination (patches of open grassland), catches of *G.f.fuscipes* were lower.

But, a problem of conversion of units arises when a comparison of light measurements from early workers is needed. Young et al. (1987) demonstrated that light units weighted for human vision (e.g. lux) are unsuitable for work on insects which have good sensitivity in the blue and U-V. Fortunately, the situation has improved with the adoption of more objective units: watts and einsteins. Also, it is more relevant to measure illumination, the amount of light falling onto an insect than luminance, the apparent brightness of lit surface to which it is exposed. Rogers (1977) measured the luminance in langleys in the vegetation. In the present study the einstein/m^2/s, a unit most appropriate alike the watt/m^2, was used.

Brady (1987) studied the light threshold of *G.m.morsitans* and found that 1690 mWm-2 is the highest intensity at which any fly took off; the sunset take-off occurred at around 350 mW/m^2. But, again, there is no universal conversion factor linking the einstein and the watt-based scales (Young *et al.*, 1987).

An indirect estimate for either sexes can be obtained through results on biotope preferences. Less light is available in bushy sites than in clear sites. In this regard, Mohamed-Ahmed et al. (1992) observed that males of *G.f.fuscipes* predominate in catches from dense vegetation and from overcast days, with females in open sites and bright days.

Essentially, these observations have been confirmed in this study. It is shown that, while the occurrence of males is determined by the presence of bushes and not much by the light regime, females are more photophilic and tend to prefer biotopes with a corridor. There is agreement here with Rogers (1977) about the light preferences and he also observed less variation in female catches with changes of vegetation. Therefore, females could comparatively be classified as more eurytopic (wider spectrum of biotopes) and mesophotic (preference of medium light), while males are more stenotopic (more biotope-selective) and euryphotic (wide light choices).

Thus, it is suggested that the lower peak of the activity curve in relation to illumination (ca. 400 $\mu E/m^2/S$) could characterize males alone, because their lower light threshold is low; and that the upper peak (ca. 1600 $\mu E/m^2/S$) is a maximum for female activity. However, it does not mean that males are absent in the upper region. While females are expected to be rare in the region below 500 $\mu E/m^2/S$, males are still active in the upper region.

Within the illumination region 1000-1600 $\mu E/m^2/S$, the biconical trap is more attractive than the pyramidal and Vavoua. Such a mechanism could be comparable to the observations of Brightwell et al. (1987). These authors found that above 31 °C the Ngu trap (NG2B) is about twice as effective for females as the biconical trap; but below 31 °C, the catch index rises sharply to reach about 11 times at 25 °C. There was a highly significant correlation between the catch and temperature on the biconical trap (Williams *et al.*, 1990) unlike the Ngu trap. It was inferred, then, that the relative failure of the F3 trap in Kenya unlike Zimbabwe had to do with this same sensitivity to temperature.

While in *G.pallidipes* the activity is most closely related with temperature, to a lesser extent with saturation deficit and least with light (Turner, 1987), light is the key factor controlling the activity of *G.f.fuscipes* (Oloo, 1983 and Mwangelwa *et al.*, 1990).

5.2.3 Light, temperature and sex-ratio

While temperature does not seem to be a determinant factor in the sex-ratio of trap catches of *G.f.fuscipes*, relative humidity plays a role with a modal value in the region 80-85% r.h., where the sex ratio varies between values as high as 2.0-4.0. Practically, no females were caught in the biconical trap during low illuminations (< 500 $\mu E/m^2/S$).

No animal is a passive respondent to environmental commands (Marler *et al.*, 1966). If circadian rythms, which serve primarily to concentrate appropriate behaviours at certain times of the day, change with temperature it would hinder accurate timing (Saunders, 1982). Accordingly, the activity of *G.f.fuscipes* depends less on temperature.

Brady and Crump (1978) showed that light sensitivity is the zeitgeber for the v-shaped activity pattern of *G.m.morsitans*. But, the shape of the activity pattern was changed with its amplitude and was affected by temperature and physiological states such as hunger.

The activity cycle of the two sexes of *G.f.fuscipes* show a peak during the mid day (Laird, 1977 and Kettle, 1991). Mohamed-ahmed et al. (1992) observed that both sexes were available to traps primarily from 0900 to 1300h. Mwangelwa (1990) and Mohamed-Ahmed and Odulaja (1997) distinguish an early male peak (ca. 0900-1000 h) from a late female peak (ca. 1400h). Gruvel (1975) also observed that the bimodal pattern of *G.tachinoides* characterized the hot seasons, whereas a unimodal pattern characterized cold and rainy seasons. The peak of activity in female *G.p.palpalis* occurred before that of males , but the opposite situation was observed in *G.p.gambiensis* and in *G.f.quanzensis* (Gouteux, 1982).

5.3. Influence of rainfall and abundance on the catchability of *G. f. fuscipes*

5.3.1 Effect of abundance on the catch index

Regarding the relationship between fly abundance and catch index, Howell (1974) reported that trap efficiency was reduced as much as 75% when a moderate-sized population of free-flying females was present to compete with caged females of the codling moth, *Laspeyresia pomonella*. Minks (1977) generalized this density-dependence of the index for sex pheromone traps. They easily detect low populations. However, when the population rises, these traps often attracts fewer moths than expected. Miller and McDouyall (1973) also found that the attractive capacity of females of the spruce budworm moth, *Chor istoneura fumiferana* decreased sharply with increasing population density.

That can be called a competition effect. The amount of pheromone emitted by the many wild females competes with the pheromone evaporating from the traps. It might not be the case of traps baited with muscalure, the sex pheromone of the housefly, *Musca domestica* which performs very well at high densities only (Carlson and Beroza, 1973). Behaviour always has a cause, and it always has one or more functions (Matthews and Matthews, 1978). There are also examples of epideictic pheromones which elicit behaviour resulting in increased spacing between conspecifics and a reduction in intraspecific competition in Coleoptera, Diptera, Homoptera, Hymenoptera, Lepidoptera and Orthoptera.

The site factor in tsetse studies is complex. The current study has shown that abundance (as measured by catch per trap per day in a reference trap) is an important element of the site factor. Therefore, in future studies it may be advantageous to define this qualitative factor by using the quantitative component abundance class (for traps used in this study: 1-9 flies per trap per day = low ; 10-19 flies per trap per day = moderate; and ≥20 flies per trap per day = high abundance).

Previously published studies were used to determine if this density-dependence of the catch index was an intrinsic characteristic of *G. f. fuscipes* populations. The number of *Glossina pallidipes* Austen caught in standard biconical traps baited with cow urine (Dransfield et al. 1986) did not show negative density-dependent relationship (Fig. 5). In this case, abundance values varied between 5 and 500 flies per trap per day and the catch index increased slightly but consistently; For example, at the abundance value of 5 flies per trap per day the catch index was 5.4 and at 100 flies flies/trap/day the index was 5.9. This trend continued for catches up to 500 flies per trap per day.

In contrast, data from Gouteux et al. (1995) on *G. f. fuscipes* in the Central African Republic ($r = -0.32$) and Mwangelwa et al. (1995) on *G. f. fuscipes* on Rusinga Island in Kenya ($r = -0.49$) show that there may be an inverse relationship between the catch index and the abundance of *G. f. fuscipes.* The reported 4-fold increase in catches of male *G. f. fuscipes* as a result of the use of cow urine compared to unbaited control in Central Africa, occurred only at a very low-abundance site (Gouteux *et al*., 1995).

5.3.2 Mechanism of Density-Dependence of Catch Index.

The mechanisms underlying this relationship between the catch index and abundance of *G. f. fuscipes* is not clear. Among other factors, trap catches of other insects may be influenced by the presence of hosts. Since tsetse are known to congregate around hosts (Fiske 1920; Chorley 1948 and Brightwell *et al*., 1992), a higher proportion of hosts might reduce the effects of artificial attractive cues associated with traps. However, it could be expected that both experimental and control traps would be influenced in the same direction under these conditions. The behavior of host animals to flies at high densities and the adaptive response of the latter may provide a possible explanation. Vale (1977) showed that the proportion of *G. m. morsitans* Westwood that engorged on an ox declined as the numbers arriving at the animal increased. Increased host grooming seemed to be responsible for this effect. Recently, Groenendijk (1996) observed that in the absence of odor, *G. pallidipes* appeared to avoid each other. It is conceivable that a modification might occur in the behavior of insects at changing densities (Minks 1977) in response to such factors. The evolution of an avoidance behavior among conspecifics at higher densities might lead to greater feeding success and survival because of reduced host grooming. Our results with dead *G. f. fuscipes* placed on traps suggest that such behavior may be operating in this tsetse species. Further research is clearly warranted to elucidate the phenomenon and its adaptive role in the insect as well as in the design of new traps. In the meantime, our results have shown that fly abundance needs to be taken into account in *G. f. fuscipes* monitoring using existing traps and in the evaluation of visual or olfactory baits of the insect.

5.3.3. Short term effect of rain on the catch index

In the present study, rain immediately caused strong fluctuations in the catch size, more conspicuously so at sites that frequently supported higher fly abundance. Rain likely stimulated the movement of flies into and away from the study sites. Therefore, it might account for high variances in trapping experiments on *G. f. fuscipes* by changing local fly abundance. These observations suggest that the chance of control by a trapping-out effect probably would be greatest during the dry season. The efficiency of traps will be increased by better visibility, because the vegetatation is poorer and also flies are expected to aggregate in the patchy thickets, where the catches will decrease faster under a trapping-out effect. Of course, some appetitive flights will persist.

During the rainy season, trap catches may decrease under the trapping-out effect, and fluctuate chaotically under the combined effects of rainfall and appetitive flight. Mwangelwa (1990) reported a fall of catches soon after the onset of rainy seasons. Higher mortality could not account satisfactorily for that phenomenon. He concluded that there was poor visibility of flies to biconical traps rather than an actual decline in the population size.

Brightwell et al (1992) indicated that during and after rains, *G.longipennis* and *G.pallidipes* extended their distribution out into open country up to 3.5 km from riverine thicket areas. Humidity rather than vegetation were the primary factors affecting the seasonal spread.

However, the population of *G.f.fuscipes* can be fairly constant (Van Vegten, 1971) and localized. nearly 80% of *G.f.fuscipes* were found during 7 weeks near the marking site (Mwangelwa, 1990; Rogers, 1977 and Gouteux, 1982).

5.4. Responses of *G.f.fuscipes* to baited traps

5.4.1 Responses to visual baits

The attractiveness of the biconical trap is the result of its colour or intensity contrast against the background. Wall and Langley (1991) reported from a comparison of 53 differently coloured cloths that royal blue gives the highest trap catch for *G.pallidipes* and *G.morsitans*. The tendency for the flies to alight was stronger with black than blue. Hence, blue traps increase the catch by maximizing the attraction with reducing the likelihood that flies just sit on their outside surface. On the other hand, the black material improves the tendency to enter the trap.

Thus, the principle that a colour with a high rate of milling should be put outside (attraction), and a colour which elicits a high landing-response be put inside to stimulate entering the trap, is confirmed in this study. The right combination suggested here for *G. f. fuscipes* is royal blue outside and peony purple inside.

5. 4.2 Responses to odour baits

The effectiveness of cow urine (Owaga, 1984) and buffalo urine (Dransfield *et al.*, 1986), as attractants was shown for *G. pallidipes* by increasing more the index than did the purified phenols (Owaga *et al.*, 1988). The evidence was such that a "standard" bait of cow urine and acetone is assumed to provide the simplest, most cost-effective odour-attractant for most species of savanna tsetse (Brightwell *et al.*, 1987); Wall and Langley (1991). Elsewhere, the total body odours of ox (Brady *et al.*, 1989), warthog (Torr, 1994 and Vale, 1977; 1979), goat, donkey, cow, bushpig (Vale, 1977) had also been tested on savanna tsetse.

But, major behavioural differences had been established between riverine and savanna tsetse species (Green, 1989). The economically important species of the palpalis group, with cosmopolitan feeding habits (Weitz, 1963 and Moloo, 1993) are often an exception for host odour specificity (Jordan, 1986). While five species of the morsitans group respond well to odours, only *G.tachinoides* responds to olfactory cues (Mérot *et al.*, 1986; Filledier *et al.*, 1988) with the possible exception of CO_2; to an extent that it was assumed that odour-guided host-location is more important among savanna species than among riverine species (Filledier *et al.*, 1988). Later on, Mérot and Filledier (1989) reported that odours emanating from man, pig and cow acted as attractants for *G.tachinoides*.

Excretory attractants bring tsetse to places which animals might frequent regularly (Groenendijk, 1996) but also considerable amounts of them are scattered on the skin from the sleeping pad and through spillage by the tail when animals are chasing away insects from the skin. Thus, they become detectable and reliable cues to find the host directly.

Electrophysiological studies by Den Otter et al (1988) showed the similarity of the sensitivity of *G.f.fuscipes* to kairomones as compared to *G.m.morsitans, G.austeni, G.p.palpalis* and *G.tachinoides*. Goes van Natters and Rinkes (1993) also showed the electrophysiological responsiveness of *G.f.fuscipes* to human sweat.

Mohamed-Ahmed et al. (1992) already mentionned the varan as an interesting candidate for odour tests on *G. f. fuscipes*. Hassanali and Saini (in prep.) obtained behavioural evidence of the effectiveness of isolated compounds from the Nile monitor in conformity with the role of this host shown by blood meals analyses

(Weitz, 1963; Moloo, 1993; Gouteux *et al.*, 1994; Okoth and Kapaata, 1990; Mohamed-Ahmed and Odulaja, 1997). Recently, Gouteux et al. (1995) tested the responses of *G. f. fuscipes* to live varan, chicken and cow urine. They noticed a significant attractiveness of the varan in the field.

Mwangelwa *et al.* (1990) obtained inconsistent results with zebu urine baits, the same successively repelling and attracting the fly. In this study, it has been shown that abundance was the factor causing such strong variations and may explain Mwangelwa's inconsistent results.

The performance of the improved visual trap (blue/red) produced in this study, was not boosted by odours. Average catch index above 3.0 was very hard to exceed. Probably, the behaviour of avoiding conspecifics could explain low indices of catches. When odour is present, colour and other visual cues are less important in attracting tsetse from a distance (Torr, 1990 and Owaga, 1985); although CO_2 boosts landing (Green, 1993) and a combination of 3-n-propyl-phenol and 4-methyl-phenol probably affects positively the trap entering response (Groenendijk, 1996).

Attempts in this study to define the optimum age of samples for crude urine attractants can be helpful in trapping. The kinetics of active compounds from cow urine (Hassanali *et al.*, 1986; Saini and Hassanali, 1992 and Okech *et al.*, 1990) are influenced, among other factors, by temperature, duration of storage and animal breeds. Temperature is rather consistent in the climate of western Kenya and eastern Uganda.

5.5. Fitness of *V.niloticus* as a host of *G.f.fuscipes*

5.5.1 Compatibility in the diel activity patterns

The diel activity pattern of *G.f.fuscipes* had been studied elsewhere. It comprises of a first peak around 0900-1000 h (Mwangelwa, 1990 and Oloo, 1983), or around 1100-1200 h (Mohamed-Ahmed and Odulaja, 1997; Laird, 1977 and Kettle, 1991) and a second peak around 1400 h, East African time. Both sexes are primarily caught in traps between 0900-1300 h (Mohamed-Ahmed *et al.*, 1992).

It was observed in this study that, between 0900-1000 h, most Nile monitors are already basking (emergence time) on tree trunks along the lakeshore. The number of monitor lizards basking at a given site remains almost constant until 1300 h. In the interval 1300-1400 h, Nile monitors go back to their burrows in tree trunks inside water. At 1500 h the numbers build up again but the afternoon peak is lower in amplitude than the morning peak. Most of the varans leave the trees at 1700-1800 h for their evening haul-in. During overcat days, the varans remain on the trees, without a mid day haul-in, performing a unimodal activity pattern.

Yeboah (1993) found that the time of emergence of *V.niloticus* when half of the varanids had come out of their burrows extended from 0720 to 1020 GMT. The mid day haul-in was also found in the bengal monitor, *varanus bengalensis* (Auffenberg, 1994) but the haul-out time by overcast time here is not as much delayed as compared to the bengal monitor. It may imply a lesser role of ambient light in the haul-out of *V.niloticus* .

Previous studies (Auffenberg, 1994), showed that water loss is greater in *V.niloticus* than in tropical skinks and geckos, which explains the preference of *V.niloticus* for living near water and for having a midday haul-in only in sunny days.

However, neither illumination nor ambient temperature, nor relative humidity seem to explain satisfactorily the mid-curve trough in the activity of *G.f.fuscipes*. It is likely dependent on a circadian clock; but in the case of the Nile monitor, it was shown in this study that the eccritic temperature (32.5°C) is reached after two hours of basking; i.e two hours after the emergence time; (It is noted that varans at a given site do not haul-out or haul-in simultaneously). Also, the strong wind which dominates the littoral zone cools down the monitor and elongates somehow its basking-sessions; after the midday haul-in in water, the varan will have cooled down and needs at a lesser extent an afternoon basking-session.

Hirth et al (1979) conducted telemetric studies on a male *V.niloticus*. Its average basking/activity temperature was 31.9 °C (range 20-37.2 °C) and the haul-out of the group took place at about 0700 h. The varan had also spent the night in water, probably snout out. Those observations in captivity in Khartoum are compatible with the findings in the present study.

Even *V.olivaceus*, in the Philippines, performs its haul-out around 0700 h and the haul-in at ca. 1700 h. But, in the latter species, the overall pattern of the daily movement is unimodal unlike other varanids whose pattern is strongly bimodal (Auffenberg, 1988).

5.5.2 Body zone preferences of *G.f.fuscipes* on the Nile monitor

G.f.fuscipes shows a significant preference for landing and feeding on the neck of the varan; yet, the neck represents only ca. 9% of the accessible upper part.

And no significant differences occur in the thickness of the skin from all the body zones. However, the largest distances between scales are found on the femoral and on the tibiotarsal regions of the limbs (3.0 mm) and on the neck (2.8mm); elsewhere, the scales are close and almost juxtaposed.

Presumably the spacing of scales is a relevant factor for the feeding response. Blood-sucking relies on the ease to insert the mouthparts through the skin and flies are likely unable to pierce the scale of the varan. Muirhead-Thompson (1991) also recognized that different species of tabanids tend to select specific areas of the body when attacking and feeding on livestock. Species with shorter mouthparts show a preference to feed on areas with short hair.

The significant increase of the landing and feeding response on the head, neck, and limbs in direct sunlight as compared to sessions under shade, suggested that reflectance plays an important role to elicit the landing-response. The observer can easily notice the ebony black look of the head, the neck and the limbs of the nile monitor during a basking-session.

Table 62: Flow chart proposed, to link the probable behavioural sequences of *G. f. fuscipes* in the process of host-finding (inspired by Wallade, S.M and Rice, M.J., 1982)

status	stimuli	consequence
HUNGER	digestive stage	APPETENCE
APPETENCE	long range stimuli (wind flow, IR, host odours)	SEARCH
SEARCH	close-range stimuli (blue lambda reflectance,shadow)	LANDING
LANDING	scale spacing of skin+intrinsic non-inhibition	FEEDING
FEEDING	host-fluid hematophago stimulants	ENGORGEMENT
ENGORGEMENT	satiation stimuli (anal evacuation)	DISENGAGEMENT
DISENGAGMENT	-------------------	FLIGHT--REST

Such a different reflectance is probably due to a differential accumulation of chromatophores in the epiderm and, also, in relation to changing scale geometry. A chart (Table 62) involving interactions of factors is proposed to explain the attraction of *G.f.fuscipes* to its hosts.

Even on a dead, defrozen monitor, the trend of the body zone choice of *G. f. fuscipes* remains fundamentally unchanged. In this case, the intensity of the landing-response is much lower, implying that although body temperature is not assumed to change considerably between the 15-minutes alternated sun/ shade sessions, sufficient skin temperature - as opposed to a cold freshly defrozen skin - is necessary to boost the landing-response.

The importance of olfactory cues in the attraction (not for body zone choice) was suggested by the results of the GC-analyses where the active compounds (Hassanali et al , in prep.) could be detected, especially compound "A"; but mainly on the head, suggesting that they occur essentially in the breath. Also, flies could land accurately with preference on holes on a perforated PvC tube at the side where the neck and head of the varan were positioned; that suggests a possibility of a dual communication mode, involving low-volatility compounds reflected by light (Alberts, 1989).

Auffenberg (1988) observed frequent intraspecific tonguing by the varans in the faeces (cloacal area), and on the head followed by the dorsal part of the neck. *G.f.fuscipes* might be sensitive to the communicative substances on the neck, where the interscale distance is maximum and may favour more their evaporation in sunlight as well as blood-sucking.

Even visual stimuli alone can be very significant in body zone choices by tsetse flies. Torr (1994) observed that, respectively 26 % and 31% of *G.m.morsitans* and *G.pallidipes* landed on the head region of an adult live warthog, and numbers increased 20 times if dark patches were fixed there. He suggested that the concentration of tsetse on the head of adult warthogs is a visual response to the dark patch produced by the preorbital glands of a mature warthog and to density-dependent changes in the grooming responses of warthogs.

In the present study, a feeding efficiency of up to 30% was observed on average (direct sunlight) on the Nile monitor. Such a feeding rate is relatively high, though in cage. Feeding bouts of ca. two minutes, on average, were observed in the field. The overall feeeding efficiency for tsetse visiting a single warthog is possibly as low as 12-18%, similar to 8% for the buffalo (Torr, 1994).

Grooming (running fast, removing tsetse with claws, hissing) was observed only in juvenile varans (less than 1kg) or in preliminary trials with big varans, where up to twenty flies were released in the experimental cage. In the field, on average 1.3 flies were seen landing simultaneously on the varan (range 1-3). No swarm was observed, in contradiction with Mwangelwa (1990) and Fiske (1920).

There was no indication in this study that the cloacal scent and the secretions of the dermal glands on the lateral line which attract conspecifics to the varan (Auffenberg, 1994) can influence the body zone choice of *G. f. fuscipes* on the varan.

5. 6. Recommendations

From the present field investigations, the following recommendations could be addressed to tsetse scientists involved in surveys and control.

1. The trapping potential of cloth fabrics for *G. f. fuscipes* can be predicted, using the blue and the infra-red components of the irradiance. This can save time and money as compared to the time-consuming tests through trapping experiments in the field.

2. Following the principle, that a strongly attractive colour should be put outside the biconical trap and a colour that elicits an intensive landing rate inside to stimulate entry into the trap,.a biconical trap with a purple target inside can boost the catches at low abundance. Such a trap is advisable in routine trapping on farms and immediately after the initial fast depletion of tsetse numbers during extermination campaigns with conventional tools. This new trap is proposed because it is usually very difficult to suppress tsetse populations at low densities.

3. A blue/red or a blue/black target is proposed *for G.f.fuscipes* instead of the usual black screen. Red was also relatively more selective to females than to males as compared to the blue/black standard and the blue target, an additional advantage in trapping.

4. More flies approached the trap in the light region 1,600-1,700 $\mu E/m^2/s$; the response of the fly became photonegative when illumination was above 1700 $\mu E/m^2/s$. The occurrence of males was determined by the presence of bushes and that of females was

very dependent on illumination, rather than vegetation type. It could be possible to minimize tsetse bites for cattle by accordingly chosing drinking or grazing-hours and places; water-fetching or swimming hours and places could also be meticulously chosen for men.

5. When the Nile monitor was present in the odour chamber of the experimental cage, flies performed an active upwind flight towards the next compartment where farther search for the host would occur. Odour baits from the Nile monitor lizard could be useful in tsetse trapping. This big lizard is also an alternative host of this fly, thus reducing bites to livestock and humans. Therefore, there is one more reason to protect this reptile.

6. There is a significant positive relationship between the number of bent dry logs of the ambatch tree, *Aeschynomene elaphroxylon* and the number of Nile monitors at sites; there is also a positive relationship between the number of Nile monitors at sites and fly catches. Tree trunks could be factors in mid-term models of tsetse colonization; monitor lizard counts could be useful in short-term models of the same.

7. Catches of *Glossina f. fuscipes* can be boosted 3-fold with acetone and cow urine at 5-6 weeks of storage.

8. Fly abundance is an important source of variation which should be taken into account in the evaluation of odour and visual baits of riverine tsetse flies. Rainfall itself likely has an immediate effect on fly abundance fluctuations.

5. 7. Suggestions for Future Study

Future research could include the following topics:

1. Intra- and interspecific variation of the responsiveness to royal blue, purple colours and reflectance of colour samples in infra-red, blue wavebands. Variants of red and blue colour could be tested as target, supported by predictions with spectro-radiometric data.
2. Further trials of the blue/red colour in riverine rather than lacustrine conditions, and in other areas including Busoga in Uganda and Central African Republic. Test of the same on *G.f.martini* and *G.f.quanzensis*.

3. Evaluate the effect of fly abundance on the catch index in other areas and if it is similar , determine thresholds at which colour-bait, urine bait (etc...) or just the standard Laveissière will be applied for control or sampling.

4. Determine the kinetics of fermentation of cow urine in relation with *G.f.fuscipes* responsivenes. Model it for several localities and breeds to know the best age for baiting.

5. Evaluate the effectiveness of illumination and biotope descriptors as possible predictors of frequency of fly bites for livestock and humans who move along water reservoirs.

6. Study the role of skin or fur colour on tsetse attacks, and body zone preference on cattle as a potential support to application of repellents.

7. Study host preferences of *G.f.fuscipes* taking account of availability, anti-tsetse grooming, abundance and distinguish preference from mere opportunism.

8. Study the bionomics of the ambatch tree, *Aeschynomene elaphroxylon* and relate it with tsetse population dynamics in an innovative perspective of farming system as tsetse control measure.

9. Compare blue/black, blue/purple, blue and black, targets and biconical traps, in control scenarios.

10. Conduct further studies on the efficacy of various levels of brightness of the top net of the biconical traps

6. SUMMARY AND CONCLUSIONS

1. Royal blue relatively attracted more flies than black colour (1.7x). The peony purple red colour stimulated significantly more landing than royal blue. Red was also relatively more selective to females than to males as compared to the blue/black standard and the blue target, an additional advantage in trapping.
2. The attractancy of trap colours was a function of reflectance in the blue ($P < 0.01$) and in the infrared ($P < 0.05$) ranges of the spectrum. However, very bright colours performed weakly both for attraction and for landing, suggesting that moderate chroma in the range 450-490 nm and in the near IR. (750-1100 nm) largely determine the attraction of this fly. The intensity of the "milling around" behaviour seems to be affected by the properties of a colour rather than a random act before landing or take-off.
3. The trapping potential of cloth fabrics for *G. f. fuscipes* was predicted, using the blue and the infra-red components of the irradiance. The landing potential was predicted by the irradiance or quantum reflectance in the blue wavebands ($r^2 = 0.98$; $P < 0.01$); attraction was predicted by the irradiance in the infra-red range ($r^2 = 0.82$; $P < 0.05$). This can save time and money as compared to the time-consuming tests through trapping experiments in the field.
4. The principle, that a strongly attractive colour should be put outside the biconical trap and, inside, a colour that elicits an intensive landing to stimulate entering the trap, was verified here. A biconical trap with the purple red component inside, caught 1.28 times more males and 1.63 times more females ($P = 0.03$; $n = 25$); an increase of up to 2.92 times at low density sites (catch of maximum 10 flies/trap/day; $P < 0.05$) was obtained.

Such a trap is advisable in routine trapping on farms and immediately after the initial fast depletion of tsetse numbers during tsetse extermination campaigns with conventional tools. This new trap is proposed because it is usually very difficult to suppress tsetse populations at low densities. A blue/red target is also proposed instead of the usual black or royal blue.

5. More flies approached the trap in the light region 1,600-1,700 $\mu E/m^2/s$; the response of the fly became photonegative when solar illumination was above 1700 $\mu E/m^2/s$. The number of males attracted was associated with the presence of bushes and that of females was very dependent on illumination, rather than vegetation.
6. *G. f. fuscipes* showed a significant preference for the neck of the monitor lizard, especially the nape of the neck (for landing and feeding; $P < 0.05$). The optimal temperature range was ca. 32-34 °C for the attraction of *G.f.fuscipes* towards the varan. There were significant differences ($P < 0.05$) between the intensity of landing in shade and under sunlight exposure on the following zones: head (mean 2.5% vs 9.1%), the neck (6.3% vs 23.1%), the femoral region of the leg (2.9 % vs 5.8 %) and the tibia region of the limb.

7. When the Nile monitor was present in the odour chamber of a compartmentalized experimental cage, traversed by a wind flow, 61.5 to 67.5% of the flies performed an active upwind flight towards the next compartment where further search for the host occurred. Only 4.2 to 15.8% of the responders abandoned the search in the second compartment. Out of 100 flies that took off from a long-range zone towards the varan, approximately 50% did so by mere ranging upwind.

8. In nature, flies tended to aggregate at sites where monitor lizards live ($r = 0.67$; $P = 0.05$ for females and $r=0.54$; $P=0.03$ or males. The flies were also seen landing on basking varans in nature. The diel activity patterns of the fly and the monitor lizard were compatible; this included the coincidence of the morning peaks and the afternoon peaks and the midday trough.
9. Four to five-week-old cow urine, in conjunction with acetone led to a significant increase of male catches (index = 4.0; $P = 0.01$; mean catch 2.6 flies/day), but not for females (index = 0.86; $P = 0.17$). However, with acetone and 5 to 6 weeks old cow urine, the highest indices occurred at sites with low abundance of tsetse (average catch 0-10 flies/trap/day), 1.70 for males and 2.32 for females ($P < 0.05$). At low abundance (0-10 flies/day) the catch index of colour or odour-baited traps was higher. A point of inflection occurred at the abundance level of 10 flies/day, where the treatment was just as good as the control trap; at high abundance (>20 flies/day) the catch index was very low (ca. 0.25). The relationship between the catch index and the abundance of flies was represented by an inverse function that could be predicted in 87% cases for females. The catch index of males was less sensitive to fly abundance.
10. Episodes of rain alone explained up to 21-87% of the total variation of the numbers caught. It suggests that rain is an important factor of dispersal. So, during the rainy season, trap catches will decrease under the trapping-out effect, and fluctuate chaotically (increase or decrease) under the effect of rain and the activity cycle of the fly. Such fluctuations will biase a latin square experiment in the field if rain is not controlled as a parameter.

11. The mechanism of the density-dependence of the catch index probably relies on the appearance of the body of congeners, because less females were caught when the number of dead flies (decoys) stuck on the trap was increased. Probably, sound or movement or epideictic pheromones also play a role in this "anti-swarming" behaviour of *G. f. fuscipes*.

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8. APPENDICES

Appendix 1: % scores when colours were tested on electric screens in the field.

variables: experiment#, colour, landing, spinning, total.

1	blublac	28.9	15.1	44.0
1	blublac	15.2	22.3	36.3
1	blublac	22.6	33.9	56.6
1	blublac	17.8	32.1	50
1	blublac	25.1	17.3	41.1
1	blublac	20.6	18.9	39.6
1	blue	19.4	12.6	32
1	blue	12.9	41.1	52.2
1	blue	10.7	12.5	23.2
1	blue	7.6	17.3	25.4
1	blue	6.8	22.4	29.3
1	black	10.6	13.2	23.8
1	black	1.1	10.5	11.3
1	black	5.6	7.5	13.2
1	black	8.9	17.8	26.7
1	black	21.1	11.5	33.3
1	black	17.2	13.7	31.0
2	blublac	17.6	61.7	79.4
2	blublac	13.6	22.7	36.3
2	blublac	28.4	34.3	62.7
2	blublac	16	37.3	53.3
2	blublac	26.8	24.3	51.2
2	orange	2.9	8.8	11.7
2	orange	25	20.4	43.1
2	orange	4.9	22.5	27.4
2	orange	4	17.3	21.3
2	orange	4.8	17	21.9
2	green	2.9	5.8	8.8
2	green	4.5	15.9	20.4
2	green	1	8.8	9.8
2	green	2.6	22.6	25.3
2	green	2.4	24.3	26.8
3	blublac	27.2	27.2	54.5
3	blublac	23.8	28.5	52.3
3	blublac	4.0	18.3	22.4
3	blublac	37.2	17.6	54.9
3	red	9	27.2	36.3
3	red	9.5	14.2	23.8
3	red	17.6	13.7	31.3

3	red	18.3	16.3	34.6
3	violet	0	9	9
3	violet	9.5	14.2	23.8
3	violet	3.2	9.8	13.7
4	blublac	16.7	28.3	45
4	blublac	21.3	50.8	62.3
4	blublac	32.5	35	72.5
4	bluwhite	5	20	25
4	bluwhite	3.3	19.7	22.9
4	bluwhite	2.5	12.5	15
4	yellow	1.7	28.3	30
4	yellow	1.6	13.1	14.7
4	yellow	2.5	10	12.5
5	blured	33.3	14.2	57.1
5	blured	42.8	14.2	57.1
5	blured	39.6	35.8	75.4
5	blured	11.7	29.4	41.1
5	blured	30.9	9.5	40.4
5	blured	24.3	21.6	45.9
5	blublac	23.8	19.0	42.8
5	blublac	28.5	14.2	42.8
5	blublac	13.2	11.3	24.5
5	blublac	41.1	17.6	58.8
5	blublac	30.9	28.5	59.5
5	blublac	40.5	13.5	54.0
6	blublared	25.9	11.1	37.0
6	blublared	32.8	30.2	63.1
6	blublared	30.3	15.1	45.4
6	blublared	22.2	22.2	44.4
6	blublac	44.4	18.5	62.9
6	blublac	22.3	14.4	36.8
6	blublac	33.3	21.2	54.5
6	blublac	25.9	29.6	55.5
7	redblac	25	8	31
7	redblac	16	33	50
7	redblac	11	19	31
7	redblac	23	26	50
7	blublac	58	8	66
7	blublac	16	33	50
7	blublac	34	34	69
7	blublac	42	7	50
8	redbrown	18	18	37
8	redbrown	31	15	46
8	redbrown	26	15	42
8	redbrown	35	30	65
8	redbrown	21	15	36

8	blublac	50	12	62
8	blublac	40	12	53
8	blublac	26	31	57
8	blublac	15	20	35
8	blublac	42	21	63
9	red	45.4	18.2	63.6
9	red	60.0	20.0	80.0
9	red	29.4	17.6	47.0
9	red	35.2	23.5	47.6
9	blue	18.2	18.2	36.3
9	blue	6.6	13.3	20
9	blue	23.5	29.4	52.9
9	blue	23.8	28.5	52.3

Appendix 2: Data when fly catches were counted before and after episodes of rain.

variables: site, occasion, count.

1	bef	6
1	bef	10
1	bef	15
1	bef	25
1	aft	21
1	aft	6
1	aft	68
1	aft	50
1	aft	60
2	bef	11
2	bef	8
2	bef	12
2	bef	6
2	aft	22
2	aft	34
2	aft	24
2	aft	13
3	bef	1
3	bef	1
3	bef	7
3	bef	1
3	aft	2
3	aft	8
3	aft	5
3	aft	6

3	aft	4
4	bef	2
4	bef	4
4	bef	12
4	bef	14
4	aft	5
4	aft	4
4	aft	18
4	aft	11
4	aft	9
5	bef	3
5	bef	3
5	bef	3
5	bef	1
5	aft	8
5	aft	12
6	bef	12
6	bef	3
6	bef	13
6	bef	8
6	aft	19
6	aft	10
6	aft	24
6	aft	8
6	aft	23
7	bef	5
7	bef	8
7	bef	3
7	bef	1
7	aft	4
7	aft	5
7	aft	2
7	aft	8
8	bef	4
8	bef	4
8	bef	12
8	bef	4
8	aft	9
8	aft	4
8	aft	2
8	aft	5
8	aft	7

Appendix 3: Data when catches were classified by vegetation density, corridors, host presence. Variables: vegetation attributes (dense?corridor? open), men, monitor lizards, males, females.

dco	1	0	5	4
dco	0	0	7	10
dco	0	0	0	2
dco	0	0	4	9
dco	0	0	1	4
dco	0	0	1	6
dco	0	0	1	3
dco	1	0	5	9
dco	0	0	7	8
dco	1	0	0	6
dco	0	0	6	3
dco	0	0	1	7
dco	0	0	5	4
dco	0	0	4	2
dco	0	0	2	3
dco	1	1	3	6
dco	0	0	3	1
dco	0	0	2	3
nco	1	0	4	4
nco	3	0	12	16
nco	3	0	5	6
nco	1	0	6	12
nco	1	1	5	5
nco	0	0	4	7
nco	1	0	4	10
nco	4	0	3	10
nco	0	0	8	8
nco	1	0	5	6
nco	0	0	4	11
nco	1	0	2	11
nco	2	1	6	7
nco	3	1	7	4
nco	2	0	8	4
nco	1	0	6	12
nco	2	0	2	6
nco	3	0	2	5
ddo	0	0	1	0
ddo	0	2	12	15
ddo	0	0	0	4
ddo	0	0	7	7

ddo	0	0	2	6
ddo	0	0	8	7
ddo	0	2	3	2
ddo	0	1	7	4
ddo	0	2	5	5
ddo	1	0	2	1
ddo	0	0	5	7
ddo	0	0	1	3
ddo	0	0	3	4
ddo	0	0	3	5
ddo	0	0	2	4
ddo	1	0	2	3
ddo	0	1	5	4
ddo	0	0	4	2
dco	0	2	9	14
dco	0	1	7	5
dco	0	0	3	1
dco	0	2	6	3
dco	0	0	1	4
dco	0	0	2	7
dco	0	0	2	6
dco	1	0	2	10
dco	2	0	0	1
dco	0	0	2	13
dco	0	0	0	2
dco	3	0	6	3
dco	1	0	4	3
dco	0	0	5	1
dco	3	0	3	3
dco	1	0	3	3
nco	0	0	2	13
nco	0	0	7	18
nco	0	4	0	6
nco	0	0	9	7
nco	2	0	1	3
nco	1	3	5	4
nco	1	1	1	5
nco	0	0	4	3
nco	1	0	2	6
nco	1	2	0	0
nco	0	3	2	1
nco	0	2	0	3
nco	1	0	3	2
nco	1	0	2	3
nco	0	0	4	0
nco	0	0	4	8

nco	3	0	3	0
nco	1	0	2	3
nco	0	0	4	11
nco	1	0	1	6
nco	0	0	1	3
nco	2	2	0	2
nco	0	0	1	2
nco	0	1	7	0
nco	0	0	0	1
nco	0	1	3	0
nco	0	0	1	0
nco	1	0	0	0
nco	2	0	0	5
nco	0	0	0	1
nco	0	0	0	0
nco	0	2	0	0
nco	0	0	0	2
nco	0	0	0	2
nco	0	0	2	5
ddo	1	0	2	0
ddo	0	1	4	6
ddo	0	0	0	2
ddo	0	3	4	0
ddo	1	0	0	1
ddo	0	0	4	6
ddo	0	1	1	4
ddo	0	0	0	3
ddo	0	10	6	2
ddo	0	1	1	0
ddo	0	0	2	2
ddo	2	0	0	0
ddo	0	4	7	2
ddo	1	0	1	0
ddo	0	2	2	1
ddo	1	2	2	1
ddo	0	0	3	6
ddo	1	0	2	2
dco	1	0	7	16
dco	2	0	2	2
dco	1	0	1	5
dco	6	12	3	4
dco	4	0	1	2
dco	6	13	7	11
dco	1	0	6	4
dco	2	1	10	7
dco	1	12	2	14

dco	3	0	3	2
dco	3	11	3	12
dco	2	0	4	12
dco	3	0	2	5
dco	2	0	1	1
dco	2	0	5	1
dco	3	0	1	7
dco	4	0	4	10
dco	1	0	3	5
ddc	1	0	3	7
ddc	0	0	2	2
ddc	1	0	1	2
ddc	0	0	0	1
ddc	0	0	0	0
ddc	0	0	1	6
ddc	0	1	1	5
ddc	0	2	1	1
ddc	0	0	2	3
ddc	0	0	0	0
ddc	0	0	0	1
ddc	2	0	4	12
ddc	0	0	0	0
ddc	0	0	0	1
ddc	0	0	2	0
ddc	1	0	0	3
ddc	0	0	4	3
ddc	0	0	1	0
ddc	0	0	4	6
ddc	0	0	1	2
ddc	0	0	0	2
ddc	0	0	0	6
ddc	0	0	0	0
ddc	0	0	1	2
ddc	0	1	3	3
ddc	0	0	0	0
ddc	1	1	1	1
ddc	1	0	1	0
ddc	0	0	0	1
ddc	0	0	0	5
ddc	1	0	0	0
ddc	0	0	0	1
ddc	0	0	0	2
ddc	1	0	0	0
ddc	1	0	1	4
ddc	0	0	1	1
dnc	0	0	10	5

dnc	0	0	1	1
dnc	0	0	1	1
dnc	0	0	0	1
dnc	0	0	0	0
dnc	0	0	1	2
dnc	0	1	3	4
dnc	0	0	1	1
dnc	0	1	0	2
dnc	0	0	0	0
dnc	0	0	0	1
dnc	0	0	0	1
dnc	0	0	2	1
dnc	0	0	0	1
dnc	0	0	1	0
dnc	0	0	0	0
dnc	0	0	0	0
dnc	0	0	1	0
dcc	0	0	2	5
dcc	0	0	4	0
dcc	0	0	2	0
dcc	0	0	0	1
dcc	0	0	1	0
dcc	0	0	3	1
dcc	0	0	2	0
dcc	0	0	0	0
dcc	0	0	1	1
dcc	0	0	0	0
dcc	0	0	4	3
dcc	0	0	0	0
dcc	0	0	1	0
dcc	0	0	0	0
dcc	0	0	2	0
dcc	0	0	0	1
dcc	0	0	1	1
dcc	0	0	0	0
dcc	0	0	12	20
dcc	1	0	9	8
dcc	0	0	4	3
dcc	0	0	1	8
dcc	0	0	0	0
dcc	0	0	10	10
dcc	0	0	10	4
dcc	0	0	7	10
dcc	0	0	11	5
dcc	0	0	3	0
dcc	1	0	9	9

dcc	0	0	6	7
dcc	0	0	4	3
dcc	0	0	1	2
dcc	0	0	3	3
dcc	0	0	7	0
dcc	0	0	2	9
dcc	0	0	2	4
dco	0	0	1	8
dco	0	2	3	1
dco	0	0	2	0
dco	2	2	3	2
dco	0	0	1	0
dco	0	0	5	2
dco	1	0	0	4
dco	0	0	4	2
dco	0	0	1	4
dco	2	0	0	0
dco	1	0	3	1
dco	1	0	0	3
dco	0	0	3	2
dco	0	0	1	1
dco	0	0	2	2
dco	1	0	5	3
dco	1	0	5	9
dco	0	0	1	0
dco	1	0	3	9
dco	0	2	10	15
dco	0	0	4	3
dco	1	5	3	7
dco	2	0	0	2
dco	2	1	7	9
dco	0	0	5	6
dco	0	0	4	2
dco	0	0	2	9
dco	1	0	1	0
dco	0	0	4	6
dco	1	0	0	4
dco	1	0	4	6
dco	0	2	1	3
dco	0	0	0	0
dco	0	0	1	4
dco	0	0	8	9
dco	0	0	1	1
dco	2	2	6	9
dco	0	0	3	6
dco	1	0	0	7

dco	1	0	6	9
dco	1	1	3	9
dco	0	4	1	9
dco	0	0	2	9
dco	1	0	2	3
dco	0	0	4	3
dco	3	0	1	9
dco	1	0	4	3
dco	0	5	0	1
dco	0	0	0	0
dco	1	0	0	2
dco	1	1	0	0
dco	0	0	1	3

Appendix 4: Data when choices of body zones by *G.fuscipes* were observed on the Nile monitor. Variables: lizard size, latency (min.), number responding, temperature range, time of day range, number engorged, duration of lizard captivity, sun exposure.

3.5	2	4	4	2	4	4	sun
3.5	7	6	2	2			sh
3.5	1	4	3	3			sh
3.5	7	1	3	4	6	4	sh
3.5	5	2	5	4	3	4	sun
3.5	13	2	5	5	0	4	sun
3.5	2	1	3	5	1	4	sh
3.5	1	6	5	6	4	4	sun
1.0	2	4	4	2	4	3	sun
1.0	5	2	5	3	1	3	sun
1.0	0.5	1	5	3	1	3	sun
1.0	6	1	4	4	1	3	sun
1.0	0.4	1	2	5	1	3	sh
1.0	0.2	6	4	5	5	3	sun
1.0	5	3	2	6	3	3	sh
1.5	5	4	5	3	3	3	sun
1.5	5	3	3	4	3	3	sh
1.5	9	3	5	4	2	3	sun
1.5	0.9	3	2	5	1	3	sh
1.5	4	8	5	5	6	3	sun
1.5	2	5	5	5	3		sun
1.5	11	1	3	6	3		sun
8.5	2	5	4	3	0	7	sun
8.5	4	5	2	4	0	7	sh
8.5	11	1	3	4	0	7	sh

8.5	6	2	5	4	0	7	sun
8.5	2	8	5	5	1	7	sun
8.5	5	5	1	6	0	7	sh
8.5	1	4	4	6	0	7	sun
8.5	0.5	3	5	3	2	8	sun
8.5	2	1	2	4	0	8	sh
8.5	1	4	2	4	0	8	sh
8.5	2	4	5	4	8		sun
8.5	0.4	5	5	5	1	8	sun
8.5	0.5	3	2	5	2	8	sh
8.5	2	5	5	6	0	8	sun
2.2	0.6	4	5	1	1	14	sun
2.2	0.5	7	5	2	5	14	sun
2.2	1	1	2	3	0	14	sh
2.2	1	6	4	3	0	14	sun
2.2	2	5	5	4	2	14	sun
2.2	13	1	2	5	1	14	sh
2.2	4	2	2	5	1	14	sh
2.2	1	3	5	5	0	14	sun
1.3	5.5	3	5	2	1	14	sun
1.3	3	5	2	3	0	14	sh
1.3	0.5	4	5	3	1	14	sun
1.3	6	4	5	3	1	14	sun
1.3	5	1	4	3	0	14	sh
1.3	0.3	2	3	4	0	14	sh
1.3	0.6	3	5	4	2	15	sun
1.3	12	1	5	2	1	15	sun
1.3	0.3	7	5	3	2	15	sun
1.3	9	1	3	3	0	15	sh
1.3	6	2	3	3	2	15	sh
1.3	1	6	4	4	5	15	sun
2.2	14.5	2	4	3	0	18	sh
2.2	0.5	8	5	3	1	18	sun
2.2	2	4	4	4	2	18	sh
2.2	0.5	6	4	4	3	18	sun
0.3	0.7	2	1	6	1	7	sun
0.3	3	1	1	6	0	7	sun
0.3	3	5	1	3	1	9	sun
0.3	2	1	1	3	1	9	sh
0.3	1.5	3	1	4	0	9	sh
0.3	0.5	4	3	4	1	9	sun
0.3	2	2	2	4	3	9	sun
3.5	1	6	6	2	0	12	sh
3.5	0.3	4	3	3	0	12	sh
3.5	2	7	5	2	1	12	sun
3.5	0.5	7	4	3	1	12	sun

3.5	4	2	2	4	3	12	sh
0.3	2.5	2	4	2	0	12	sun
0.3	8	1	2	2	1	12	sh
0.3	1.5	1	3	2	1	12	sh
0.3	6	1	5	3	0	12	sun
0.3	0.3	7	5	3	3	12	sun
0.3	5	1	1	3	1	12	sh
3.5	6	3	5	2	0	14	sun
3.5	1	4	2	2	3	14	sh
3.5	.	4	2	2	1	14	sh
3.5	0.2	8	4	2	2	14	sun
3.5	10	1	3	3	1	14	sun
3.5	3	5	2	3	1	14	sh
3.5	4	4	1	4	2	14	sh
3.5	.	6	5	4	1	14	sun

Appendix 5: Data when basking monitor lizards were hourly counted to evaluate their availability as a host for the fly. Variables: time interval, total, lying up on a tree, up with head raised, climbing up, moving downward, in shade, swimming, on land, on floating trunk, coming from the burrow, entering into the burrow, low on a tree, weather.

1	11	2	1	2	1	0	1	0	4	0	0	0	dull
1	3	2	1	0	0	0	0	0	0	0	0	0	sun
1	4	2	1	1	0	0	0	0	0	0	0	0	dull
1	2	1	0	0	0	0	0	0	0	0	0	1	dull
1	2	0	0	1	0	0	0	0	0	1	0	0	dull
1	4	0	0	3	0	0	0	1	0	0	0	0	sun
2	4	3	0	0	0	0	0	0	0	0	0	1	sun
2	7	3	1	0	1	0	0	0	1	1	0	0	dull
2	6	6	0	0	0	0	0	0	0	0	0	0	dull
2	5	4	0	0	0	0	0	0	0	0	0	1	sun
2	4	2	0	1	0	0	0	0	0	0	0	1	sun
2	4	2	1	0	0	0	1	0	0	0	0	0	sun
2	10	5	0	2	1	0	0	0	0	0	0	3	sun
3	5	3	0	0	1	0	0	0	1	0	0	0	sun
3	5	2	0	1	0	0	0	0	1	0	0	1	dull
3	2	1	1	0	0	0	0	0	0	0	0	0	sun
3	9	7	0	1	0	0	0	0	1	0	0	0	dull
3	6	3	0	1	0	0	0	0	2	0	0	0	sun
3	7	4	0	1	0	1	0	0	0	0	0	1	sun
3	14	4	1	2	1	0	2	1	3	0	0	0	dull
4	8	5	0	0	1	0	0	0	0	0	0	2	sun
4	7	3	0	2	0	0	0	1	0	0	0	1	sun
4	8	5	0	2	0	0	1	0	0	0	0	0	dull
4	8	6	0	0	0	0	0	0	2	0	0	0	dull
4	7	4	0	9	0	0	0	0	0	0	0	3	sun
4	5	3	0	1	0	0	0	0	1	0	0	0	sun
4	5	1	0	0	0	3	0	0	0	0	0	1	sun
5	3	0	0	0	0	2	0	1	0	0	0	0	sun
5	4	3	1	0	0	0	0	0	0	0	0	1	dull

5	5	3	0	0	2	0	0	0	0	0	0	0	sun
5	8	7	0	0	0	0	0	0	0	0	0	1	dull
5	8	6	1	0	0	0	0	0	1	0	0	0	sun
5	5	0	0	0	2	1	0	1	0	0	0	1	sun
5	11	3	2	1	1	0	1	0	2	0	0	2	dull
5	6	3	0	0	0	2	0	0	0	0	0	1	sun
6	4	0	0	0	0	1	0	1	0	0	0	2	sun
6	4	0	0	1	0	0	0	1	0	0	0	1	sun
6	9	3	1	1	3	0	0	0	1	0	0	0	dull
6	11	8	0	0	2	0	0	0	1	0	0	0	dull
6	3	1	0	0	1	0	0	0	0	0	0	1	sun
6	2	0	0	0	0	1	0	1	0	0	0	0	sun
6	3	0	0	0	0	2	0	0	1	0	0	0	sun
6	3	0	0	0	0	2	0	0	1	0	0	0	sun
6	7	0	0	0	2	2	0	0	0	0	0	3	sun
7	7	0	0	0	1	1	0	2	0	0	0	3	sun
7	5	0	0	0	1	2	0	0	0	1	0	1	sun
7	4	0	1	0	0	1	0	2	0	0	0	0	sun
7	6	2	1	0	1	0	0	0	2	0	0	0	dull
7	7	4	0	0	0	1	0	1	1	0	0	0	sun
7	5	0	0	0	1	2	0	0	1	0	0	1	sun
7	11	9	0	0	0	0	0	1	1	0	0	0	dull
7	7	2	0	0	0	0	1	2	1	0	0	1	sun
8	4	0	0	0	0	0	0	3	0	0	0	1	sun
8	6	1	0	1	0	1	0	1	1	0	0	1	sun
8	6	0	1	0	0	2	0	0	2	0	0	1	sun
8	6	3	2	0	0	0	0	0	1	0	0	0	dull
8	7	5	1	0	0	0	0	0	1	0	0	0	dull
8	2	1	0	0	0	0	0	1	0	0	0	0	sun
9	9	8	0	0	1	0	0	0	0	0	0	0	dull
9	10	6	0	0	1	0	1	0	2	0	0	0	sun
9	7	3	1	0	2	0	0	0	1	0	0	0	dull
9	4	2	0	0	0	0	0	1	0	0	0	1	sun
9	4	1	0	0	0	1	0	1	1	0	0	1	sun
9	4	2	0	0	0	0	0	0	1	0	0	1	dull
9	4	0	0	0	1	0	0	2	0	0	0	1	sun
10	3	1	0	0	1	0	0	0	1	0	0	0	sun
10	4	3	0	0	0	0	0	0	1	0	0	0	dull
10	4	1	0	0	0	0	0	0	2	0	0	1	sun
10	4	2	0	0	1	0	0	0	0	0	0	1	sun
10	9	4	2	0	0	0	0	0	3	0	0	0	dull
10	5	3	1	0	0	0	0	0	0	0	0	0	dull
10	6	4	1	0	0	0	1	0	0	0	0	0	sun
10	4	3	0	0	0	0	0	0	0	0	1	0	dull
10	6	5	0	0	0	0	0	0	0	0	1	1	dull
10	3	0	0	0	1	0	0	0	1	0	0	1	sun
10	4	0	1	0	1	0	0	0	2	0	0	0	sun
11	5	5	0	0	0	0	0	0	0	0	0	0	dull
11	3	3	0	0	0	0	0	0	0	0	0	0	dull
11	6	5	0	0	1	0	0	0	0	0	0	0	sun
11	4	3	1	0	0	0	0	0	0	0	0	0	dull
11	5	2	0	0	2	0	0	0	1	0	0	0	dull

Appendix 6: Data when a biconical trap with red (peony purple) inside was compared to the standard biconical trap. Variables: site, day, sex or total, catch in experimental trap, catch in control, abundance class (1= ≥20 flies/day in standard trap; 2 = ≥10 flies/day;3 = < 10 flies/day).

1	1	m	15	19	2
1	2	m	16	27	1
1	1	f	10	49	1
1	2	f	28	23	1
1	1	t	25	68	1
1	2	t	44	50	1
2	1	m	1	2	3
2	2	m	2	10	2
2	1	f	5	6	3
2	2	f	12	34	1
2	1	t	5	6	3
2	2	t	12	34	1
3	1	m	12	34	1
3	2	m	3	1	3
3	1	f	10	4	3
3	2	f	8	4	3
3	1	t	13	5	3
3	2	t	12	6	3
4	1	m	7	1	3
4	2	m	8	9	3
4	1	f	10	4	3
4	2	f	10	9	3
4	1	t	16	4	3
4	2	t	18	18	2
5	1	m	2	1	3
5	2	m	0	1	3
5	1	f	10	1	3
5	2	f	11	7	3
5	1	t	11	1	3
5	2	t	11	8	3
6	1	m	1	4	3
6	2	m	8	4	3
6	1	f	13	15	2
6	2	f	22	6	3
6	1	t	14	19	2
6	2	t	30	10	2
7	1	m	3	2	3

7	2	m	4	3	3
7	1	f	7	1	3
7	2	f	6	5	3
7	1	t	9	2	3
7	2	t	10	8	3
8	1	m	1	1	3
8	2	m	1	1	3
8	1	f	7	1	3
8	2	f	3	4	3
8	1	t	8	2	3
8	2	t	4	5	3
9	1	m	7	5	3
9	2	m	29	21	1
9	1	f	7	3	3
9	2	f	34	19	2
9	1	t	14	8	3
9	2	t	63	40	1
10	1	m	11	3	3
10	2	m	8	11	2
10	1	f	8	2	3
10	2	f	14	13	2
10	1	t	19	5	3
10	2	t	22	24	1

Appendix 7: Data when cow urine of 3-4 weeks was used as a bait on a biconical trap with a peony purple (red) target inside. variables: trap site males females.

red	7	0	8
blue	8	1	3
red	3	4	2
blue	4	2	2
blue	7	0	7
red	8	1	4
red	1	17	6
blue	2	35	46
blue	3	1	5
red	4	4	6
red	7	5	14
blue	8	1	5
blue	1	11	6
red	2	4	2
red	3	4	4
blue	4	3	3

red	5	1	0
blue	6	1	11
blue	7	3	10
red	8	1	4
red	1	7	6
blue	2	8	22
blue	5	1	10
red	6	1	17
red	7	0	7
blue	8	0	3
blue	1	9	8
red	2	12	16
blue	3	1	1
red	4	5	7
red	5	0	4
blue	6	1	27
blue	7	2	3
red	8	3	5
red	3	5	7
blue	4	0	2
blue	5	3	1
red	6	0	17
red	7	4	11
blue	8	1	3
red	1	4	2
blue	2	7	18
blue	3	2	5
red	4	5	7
red	5	1	6
blue	6	1	12
blue	7	3	6
red	8	5	2
blue	1	17	20
red	2	11	4
red	3	4	3
blue	4	1	1
blue	5	0	4
red	6	4	11
red	7	2	13
blue	8	2	2

Appendix 8: Data when white and black top nets were compared on the biconical trap with a purple red target inside; or with an extra black portion outside. variables: experiment, trap, site, males, females, day, replicate, total catch, abundance class.

1	whitred	2	7	21	1	1	28	2
1	blacred	1	9	11	1	1	20	2
3	whitred	3	14	51	1	1	65	2
3	blblred	4	1	5	1	1	6	2
1	whitred	1	3	5	2	1	8	1
1	blacred	2	11	42	2	1	53	1
3	whitred	4	9	21	2	1	30	2
3	blblred	3	6	17	2	1	23	2
1	whitred	2	3	19	3	2	22	2
1	blacred	1	0	16	3	2	16	2
3	whitred	3	8	33	3	2	41	2
3	blblred	4	5	9	3	2	14	2
3	whitred	4	2	4	4	2	6	1
3	blblred	3	6	11	4	2	17	1
1	whitred	2	6	10	5	3	16	2
1	blacred	1	2	7	5	3	9	2
3	whitred	3	8	14	5	3	22	2
3	blblred	4	3	7	5	3	10	2
1	whitred	1	5	12	6	3	17	2
1	blacred	2	9	16	6	3	25	2
3	whitred	4	5	19	6	3	24	2
3	blblred	3	3	5	6	3	8	2
1	whitred	2	0	5	6	3	5	1
1	blacred	1	2	8	6	3	10	1
3	whitred	3	7	23	6	3	30	2
3	blblred	4	2	6	6	3	8	2
1	whitred	1	7	15	6	3	22	2
1	blacred	2	13	46	6	3	59	2
3	whitred	4	7	18	6	3	25	2
3	blblred	3	2	6	6	3	8	2
2	ctrl	7	5	8	1	1	13	2
2	blacred	8	2	13	1	1	15	2
2	ctrl	10	0	10	1	1	10	1
2	blacred	9	19	28	1	1	47	1
2	ctrl	5	9	18	2	1	27	2
2	blacred	6	13	34	2	1	47	2
2	ctrl	9	15	24	2	1	39	2
2	blacred	10	7	10	2	1	17	2
2	ctrl	6	4	24	3	2	28	2

2	blacred	5	1	15	3	2	16	2
2	ctrl	7	9	17	3	2	26	2
2	blacred	8	7	13	3	2	20	2
2	ctrl	10	2	9	3	2	11	2
2	blacred	9	0	5	3	2	5	2
2	ctrl	8	4	10	4	2	14	2
2	blacred	7	1	7	4	2	8	2
2	ctrl	9	1	6	4	2	7	1
2	blacred	10	9	9	4	2	18	1
2	ctrl	6	9	16	5	3	25	2
2	blacred	5	5	12	5	3	17	2
2	ctrl	7	2	9	5	3	11	2
2	blacred	8	1	6	5	3	7	2
2	ctrl	10	4	8	5	3	12	2
2	blacred	9	7	13	5	3	20	2
2	ctrl	5	7	17	6	3	24	2
2	blacred	6	2	8	6	3	10	2
2	ctrl	8	8	6	6	3	14	2
2	blacred	7	2	11	6	3	13	2
2	ctrl	6	6	12	6	3	18	2
2	blacred	5	0	2	6	3	2	2
2	ctrl	7	5	14	6	3	19	2
2	blacred	8	5	8	6	3	13	2
2	ctrl	5	8	10	6	3	18	2
2	blacred	6	11	24	6	3	35	2
2	ctrl	8	6	13	6	3	19	2
2	blacred	7	3	5	6	3	8	2
2	ctrl	9	12	27	6	3	39	2
2	blacred	10	9	14	6	3	23	2

Appendix 9: Catches in standard pyramidal blue/black and in a pyramidal blue/red - (Turkey red; n = 7) set on a discontinuous lakeshore vegetation with a large open corridor .

sex or total	mean ± SE	Kolmogorov score prob
male	7.0±2.14	
	2.7±0.77	0.39 K
female	11.3±5.82	
	8.4±3.35	0.66
total	18.3±7.45	
	11.1±3.89	0.39

Appendix 10: Catches in standard pyramidal blue/black (n = 6) and in a pyramidal blue/red (Turkey red; n = 8) set on a continuous linear lakeshore vegetation with open background

sex or total	mean ± SE	Kolmogorov score prob
male	5.0 ± 1.98	
	3.6 ± 1.13	0.53
female	16.1 ± 3.24	
	8.7 ± 2.83	0.11
total	21.1 ± 3.65	
	12.3 ± 3.55	0.11

Appendix 11: Catches in standard pyramidal blue/black (n = 6) and a pyramidal blue/red (Turkey red; n = 7) set on a discontinuous linear lakeshore vegetation with a banana field on background

sex or total	mean ± SE	Kolmogorov score prob
male	2.7 ± 0.52	
	2.6 ± 0.55	0.95
female	7.5 ± 1.65	
	5.0 ± 3.07	0.45
total	10.2 ± 1.94	
	7.6 ± 3.57	0.51

Appendix 12: Catches in standard biconical trap and in biconical with blue and red on the outer side (Doge purple; n = 5) set on a very bushy site 200 m away from lakeshore

sex or total	mean ± SE	T-test prob.
male	29.0 ± 13.5	
	16.2 ± 3.5	0.21 ns
female	9.7 ± 5.8	
	1.6 ± 1.1	0.51 ns (K)
total	38.7 ± 5.8	
	17.8 ± 10.3	P = 0.02 *

Appendix 13: Catches in standard biconical trap and in biconical with blue and red inside (Doge purple; n = 3) set on a discontinuous linear lakeshore vegetation with slightly bushy background

sex or total	mean ± SE	T-test prob.
male	8.0 ± 1.52	
	5.0 ± 4.04	0.52
female	5.0 ± 1.00	
	2.3 ± 0.33	0.06
total	13.0 ± 2.30	
	7.3 ± 3.92	0.28

Appendix 14: Catches in standard biconical trap and in biconical with blue and red inside (Doge purple; n = 3) set on a discontinuous linear lakeshore vegetation with very bushy background

sex or total	mean ± SE	T-test prob.
male	6.3 ± 0.33	
	7.0 ± 3.05	0.51
female	9.3 ± 3.38	
	3.0 ± 1.73	0.17
total	15.6 ± 3.17	
	10.0 ± 1.52	0.18

Appendix 15: Catches in standard pyramidal blue/black (n = 6) and a pyramidal blue/red (Doge purple; n = 7) set on a discontinuous linear lakeshore vegetation with an open background.

sex or total	mean ± SE	T-test prob.
male	10.1 ± 3.19	
	5.0 ± 1.22	0.24 K
female	8.5 ± 1.64	
	4.8 ± 1.77	0.16
total	18.6 ± 4.34	
	9.8 ± 2.13	0.12

Appendix 16: Catches in standard biconical trap and in biconical with blue and red inside (Peony purple; n = 4) set on a discontinuous linear lakeshore vegetation with a slightly bushy background

sex or total	mean ± SE	T-test prob.
male	17.7 ± 4.38	
	19.2 ± 4.76	0.82
female	12.2 ± 4.02	
	14.7 ± 6.44	0.75
total	30.0 ± 7.49	
	34.0 ±10.49	0.76

Appendix 17: Catches in standard biconical trap and in biconical with blue and red on the outer side (Peony purple; n= 5) set at a site with high grass and a slight corridor 20 m from the lakeshore.

sex or total	mean ± SE	T-test prob.
male	17.8 ± 3.91	
	10.0 ± 3.34	0.16
female	7.0 ± 1.64	
	4.2 ± 1.56	0.25
total	24.8 ±11.88	
	14.2 ± 10.9	0.18

Appendix 18: Catches in standard biconical trap and in biconical with blue and red on the outer side (Peony purple; n = 5) set on a discontinuous linear lakeshore vegetation with banana field in background

sex or total	mean ± SE	T-test prob.
male	4.0 ± 0.94	
	2.6 ± 1.53	0.46
female	3.2 ± 0.73	
	2.8 ± 1.15	0.77
total	7.2 ± 0.86	
	5.4 ± 1.80	0.39

Appendix 19: Responses of *G. f. fuscipes* to zebu urine (4 weeks) and acetone on blue/black biconical traps in Kisui area on sites with a high density of flies. Sites with similar effects are pooled.Effect 1= attraction; effect 2 = repellency; males; females;

Effect	control	baited trap	n	prob.	index
increase	6.8 ± 0.87	10.3 ± 1.68	9	0.18	1.50
	16.5 ± 1.97	23.0 ± 3.37	9	0.30	1.38
decrease	10.6 ± 2.41	9.2 ± 2.37	9	0.90	0.86
	19.8 ± 3.50	18.0 ± 4.61	9	0.48	0.90

GLOSSARY OF SPECIAL TERMS

Abundance was measured by the catch/trap/day in the control trap. **Density**, which indicates the number of flies per unit area was not measured.

Active compounds: attractants, chemical compounds that mediate host-seeking behaviour.

Catch index: the ratio (catch in the experimental trap/ catch in control trap)

Cues: stimuli, active signals which elicit behaviour.

Decoy = lure, deception, fake; dead flies used as "decoys" are an imitation of flies landing on the trap.

Eccritic temperature: is the preferred body temperature of a lizard. Once it is reached, the lizard reduces the amount of absorbed solar energy (e.g) by changing posture.

haul-out time: time of day when the Nile monitor comes out of its burrow; the lizard goes back into its burrow at the **haul-in time**.

Hue: is defined by the dominant wavelength (i.e., blue 450-490 nm). A **chromatic** colour is one possessing a hue , i.e., green; an **achromatic** colour is one without a hue, i.e., white or grey.

Infra-red radiation is generated by vibration and rotation of atoms and molecules in any substances with a temperature above absolute zero. Because IR band falls between the bands of light and radio ($0.75 - 10^3\ \mu$), it may be focused by lenses and yet can be transmitted like radar and radio through materials that block visible light. The interest of an IR communication system could rely on the fact that the chances of an insect's antenna, over any distance, colliding with thinly scattered molecules are far less than the chance of the antenna passing through the electromagnetic field of the molecule.

Latency : time elapsed before a given behaviour starts

Quantum reflectance refers to the number of quanta reflected/nm within a wavelength range (e.g.) blue range. The integrate command (IT) of the spectroradiometer performs an integration over a specified wavelength range in a single data file.

Range: tsetse take off generally upwind when stimulated by host odour (**long-range**). The activity of **searching** for a plume or the flight in the absence of host stimuli is called **ranging**.Near an odour source, tsetse divert to visual objects (**close-range**).

Reflectance (%): the illumination caused by a focused beam of radiation reflected from a sample material as compared to that reflected from the white reference material.

silhouette: outline, image, profile, shadow, shape, contour, dark shape.

Publications from this thesis

1. Muhigwa J-B. B.and Saini, R. K. 1997: Responses of *Glossina f. fuscipes* Newstead to host odour baits in the field, p. 170. H.G. Robertson [ed.] In Proceedings , ESSA-AAIS Congress, Stellenbosch, 30 June - 4 July, Entomol. Soc. South Africa
2. Muhigwa, J-B. B., R.K.Saini and A. Hassanali, 1998: Effects of fly abundance on catch Index of Traps for *G. f. fuscipes* (Diptera, Glossinidae), Journal of Medical Entomology. **35(2):** 00-00.
3. Muhigwa, J-B. B., R. K.Saini and A. Hassanali. 1998: The colour preferences of *Glossina f. fuscipes.* Journal of African Zoology. In the press
4. Muhigwa, J-B. B., R. K.Saini and A. Hassanali. 1998: Responses of *G. f. fuscipes* to the Nile monitor lizard (*Varanus niloticus)* as a host. Journal of African Zoology. In the press
5. Muhigwa, J-B. B. 1998: Diel activity pattern and biotope choices of the Nile monitor lizard, *Varanus niloticus.* African Journal of Ecology. **36**: 00-00.

Manuscripts on *Glossina f. fuscipes* in prep. (internal review at ICIPE):

- Optimum age of storage of cow urine baits for *G. f. fuscipes*
- Detailed behaviour of *G. f. fuscipes* around its conventional traps in relation with weather
- Body zone preferences of ticks on the Nile monitor lizard