Effect of defensive behaviour by cattle on the feeding success and nutritional state of the tsetse fly, *Glossina pallidipes* (Diptera: Glossinidae)

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Abstract

Two experiments were conducted at Galana Ranch, Kenya, which examined, under natural conditions, the relationships between the number of tsetse flies (*Glossina pallidipes* Austen) attracted to cattle, the rate at which the cattle made defensive movements, and the feeding success of the tsetse. The most frequent defensive movements were skin ripples and tail swishes, while leg kicks were of intermediate frequency, and head and ear movements were infrequent. In one experiment, the rate of skin ripples, but no other type of defensive movement, was significantly correlated with the number of tsetse attracted to the cattle. The proportion of tsetse that engorged was significantly ($P < 0.004$) correlated with the rate of leg kicks, more weakly with the rate of head movements ($P < 0.07$), and uncorrelated with the rates of other types of defensive movement. In the second experiment, the rates of skin ripples, tail swishes and leg kicks were significantly correlated with the number of tsetse attracted to the cattle. The proportion of tsetse that engorged was again significantly correlated to the rate of leg kicks ($P < 0.03$), more weakly to the rate of head movements ($P < 0.04$), and unrelated to the rates of other types of defensive movement. In neither experiment was there a significant relationship between the number of tsetse attracted to the cattle and the proportion that engorged, suggesting that any density-dependent feeding success was too weak to be detected. In experiment 1, the relative fat content of the male *G. pallidipes* that fed decreased as the rate of leg kicks increased, suggesting that when hosts are more active the sub-sample of tsetse that feed, out of those that approach, is both smaller and hungrier. There was no detectable effect of host defensive behaviour on the bloodmeal size of male *G. pallidipes*.

Introduction

Birds and mammals exhibit defensive behaviours when under attack by blood-sucking insects and the rate at which such behaviours are made is often a function of the number of attacking insects (Edman *et al.*, 1972; Waage & Nondo, 1982). Experiments with restrained animals, or comparisons among several host species, have shown in turn that higher rates of defensive behaviour may lead to a reduction in the ability of the insects to obtain blood meals (Edman & Kale,

1971; Edman *et al.*, 1972, 1974; Klowden & Lea, 1979; Waage & Nondo, 1982). Combining these effects suggests that host defensive behaviour may lead to density-dependent feeding success in blood-sucking insects, that is, an inverse relationship between the number of insects attracted to a host and the feeding success of the insects, which in turn may contribute to density-dependent mortality of the insects, or lead to host switching. Direct competition among insects for feeding sites might also lead to density-dependent feeding success in a manner independent of host defensive behaviour. Density-dependent feeding success was demonstrated for mosquitoes feeding on ciconiiform birds (Edman *et al.*, 1972), but not for mosquitoes feeding on humans (Charlwood *et al.*, 1995).

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Patterns similar to those described above have been found for tsetse flies (Diptera: Glossinidae). Several studies have reported that a greater density of tsetse leads to higher levels of host activity (Vale, 1977; Baylis et al., 1994; Torr, 1994), and that higher levels of host activity lead to a decrease in tsetse feeding success (Vale, 1977; Baylis et al., 1994; Baylis & Mbwabi, 1995a). Nevertheless, statistical examination of the relationship between the density of tsetse and their feeding success suggests that density-dependence is either weak or non-existent: Vale (1977) reported weak density-dependence in four out of 12 studies; Baylis et al. (1994) suspected weak density-dependence but the relationship was not significant; Torr (1994) and Baylis & Mbwabi (1995a) found no evidence for density-dependence.

Defensive movements can be categorized into several types, such as leg kicks, tail swishes, skin ripples, etc. Previous workers (except Torr, 1994) have tended to use the total of all such movements in analyses, perhaps because this seems intuitively the most relevant variable to the feeding success of the insects. However, blood-sucking insects often show marked preferences for landing on certain parts of a host's body, and these preferences vary with both insect and host species. For example, the tsetse fly Glossina pallidipes Austen (Diptera: Glossinidae) tends to land on the lower legs of cattle, while G. m. morsitans Westwood prefers the belly and back (Thomson, 1987). In contrast to their landing preferences on cattle, these two species tend to land on the back and face of warthogs (Torr, 1994).

These observations suggest that the relationship between tsetse density, host defensive behaviour and tsetse feeding success may be more complex than it at first appears. Here, this relationship is examined for two recent studies of the feeding behaviour of G. pallidipes on cattle in Kenya: experiment 1, a comparison of uninfected and Trypanosoma-infected cattle (Baylis & Mbwabi, 1995a); and experiment 2, a comparison of untreated cattle with cattle treated with certain pyrethroid pour-ons (Baylis et al., 1994). In addition to effects on feeding success, it is possible that host defensive behaviour, by presenting an obstacle to feeding, may affect the hunger stage or the size of the bloodmeals of the population of tsetse that feed. These relationships are examined for the tsetse caught in experiment 1.

Materials and methods

Experiments were carried out at Galana Ranch, a 6000 km² cattle ranch in south-eastern Kenya (39–40°E, 2–3°S), bordered to the west by Tsavo East National Park, and to the south by the Sabaki River. The ranch is semi-arid with large numbers of G. pallidipes found in the wetter eastern zone where there is dense, coastal vegetation.

The cattle used in the experiments were Orma Boran cows or heifers, selected from the Orma Breeding Herd of Galana Ranch. Twenty-four cattle were examined for each experiment. Each day one cow or heifer was placed in a pen constructed from widely-spaced metal bars, of total size 2.0×0.7×1.5 m (l×w×h). The pen was surrounded by an incomplete ring of electric nets (Vale, 1974) which sampled approaching and departing flies. Each net was a 1.5×1.5 m square of fine black netting, covered on both sides with a grid of electrocuting wires. Six nets covered approximately one third of the circumference of a circle around the animal. They were operated from 16.00–18.00 h (experiment 1) or

16.00–18.10 h (experiment 2). These periods represent the peak activity times of G. pallidipes at Galana Ranch (M. Baylis & M.L. Warnes, unpublished data). Tsetse that collided with the nets were killed or stunned (although some may have escaped: Packer & Brady, 1990) and fell into 2×1 m trays containing water and detergent, which were placed at the base of both the inner and outer faces of each net. Further details of the experimental designs are given in Baylis et al. (1994) and Baylis & Mbwabi (1995a).

Each cow or heifer was watched side-on from a distance of 20–30 m using binoculars and defensive movements were recorded. The five movements included in this category were tail swishes, leg kicks, skin ripples, head swings or shakes, and ear flaps. Since the cattle were watched from one side only, skin ripples on the distant side were not visible, and were not recorded. It was not feasible to observe the cattle for the duration of the experiment each day, and a 20 minute period only, from 17.30–17.50 h, was selected.

At the end of each experiment the rectal temperature of the cow or heifer was measured, and a sample of blood was collected from an ear-vein for estimation of the packed cell volume (PCV).

Controls

To find out whether fed flies were caught in the absence of a cow or heifer, the experiments were run with an odour-baited 2×1 m black target in the crush (Baylis et al., 1994; Baylis & Mbwabi, 1995a). Overall, only three out of a total of 160 flies (1.9%) were found with small traces of fresh blood, and no flies with large bloodmeals were caught.

Predictions from experimental design

In both experiments, the electric nets covered one-third of the circumference of a circle around the cow or heifer. From the assumptions given by Vale (1977) about the use of electric nets, several predictions can be made: (i) one-third of all tsetse that approach the animal will be caught on the outer faces of the electric nets; (ii) the remaining two-thirds of approaching tsetse reach the animal; of these, one-third will be caught on the inner faces of the electric nets as they depart; (iii) therefore, the ratio of tsetse caught on the outside:inside of the electric nets should be 3:2 (i.e. three-ninths versus two-ninths of approaching tsetse); and (iv) all fed flies should be caught on the inner faces of the electric nets.

Calculation of variables

Several variables were calculated for each cow or heifer: (i) ox-catch: the total number of G. pallidipes caught by the electric nets, used here as a measure of the number of tsetse attracted to the cattle; (ii) skin, tail, leg, head, ear and total movement rates: the mean number of such defensive movements made by the cattle per minute; and (iii) proportion-engorged: the proportion of ox-catch classified as fed, and used here as a relative measure of the feeding success of G. pallidipes on each cow or heifer. Note that proportion-engorged gives lower values than the measure of feeding success used by Vale (1977) because it includes tsetse caught by the electric nets before having reached the animal; however, it is satisfactory for comparative purposes (see discussion).

Table 1. Detransformed means and 95% confidence limits (C.L.) of the number of *Glossina pallidipes* caught around cattle (ox-catch), the number of defensive movements made by the cattle per minute (movement rate), and the proportion of *G. pallidipes* that fed on the cattle (proportion-engorged). Differences between means of the two experiments were tested by ANOVA.

Parameter		Experiment 1 N=23		Experiment 2 N=24		
	mean	95% C.L.	mean	95% C.L.		
Ox-catch					$F_{1,45}=32.5, P < 0.001$	
Movement rate					$F_{1,45}=40.0, P < 0.001$	
Proportion-engorged[1]					$F_{1,36}=0.02$, n.s.	

[1]Nine *T. congolense* infected cattle in experiment 1 are excluded.
n.s. not significant.

Nutritional analyses

All male *G. pallidipes* collected in experiment 1 were dried at 55°C and sent to the Department of Veterinary Medicine, University of Bristol, or Insect Investigations Limited, (Department of Veterinary Medicine, University of Bristol) where their lipid and haematin contents were measured using the methods described by Ford *et al.* (1972) and Langley *et al.* (1990). Female flies were not analysed. This paper reports on the fat and haematin contents of the recently fed flies only.

Data analysis

Prior to statistical analysis, data were transformed to remove relationships between means and variances (Southwood, 1978) or normalize distributions (Sokal & Rohlf, 1981); ox-catch was square-root transformed; movement rates were $\ln(n+1)$ transformed; and proportion-engorged was arcsine $\sqrt{}$ transformed. Means, and 95% confidence limits, were detransformed for presentation (Zar, 1984). Tukey's test (Zar, 1984) was used to determine significant differences between means in multiple comparisons.

Baylis & Mbwabi (1995a) report that tsetse feeding success is greater if cattle are infected with *T. congolense* Broden and attribute this to vasodilation in the infected cattle. Experiment 1 included cattle infected with *T. congolense*; experiment 2 did not. For the comparison of the feeding successes of tsetse in the two experiments, only non-*T. congolense* infected cattle were included. Baylis & Mbwabi (1995a) found no difference in the rate of defensive movements of infected and uninfected cattle, and therefore infected cattle are included in other analyses. Additionally, one cow in experiment 1 escaped from the pen; data for this animal are excluded from all analyses. Experiment 2 included cattle that were untreated, or treated with certain insecticidal

pour-ons. The pour-ons were not found to affect the rate of defensive movements of the cattle or the feeding success of the tsetse (Baylis *et al.*, 1994), and therefore these treatments are ignored in the analyses presented here.

Results

Experiment 1 was performed during February–March and experiment 2 between May–July 1993. At Galana Ranch, *G. pallidipes* are generally most abundant early in the year; for this reason, the number of tsetse flies attracted to the cattle during experiment 1 was significantly greater than during experiment 2 (table 1). Similarly, the total rate of defensive movements made by the cattle was significantly greater in experiment 1 than experiment 2 (table 1). However, there was no significant difference in the proportion of tsetse that engorged (table 1).

Behaviour of tsetse around electric nets

In experiment 1, a total of 1597 tsetse were caught on the outer faces of the electric nets, and 1466 on the inner faces (difference from 3:2 ratio: $\chi^2=79.0, P < 0.001$). In experiment 2, the catches were 844 and 822 respectively ($\chi^2=59.5, P < 0.001$). Therefore, an unexpectedly high proportion of tsetse were caught on the inside of the electric nets. Furthermore, 176 out of 752 (23.4%, experiment 1) and 54 out of 307 (14.6%, experiment 2) fed tsetse were caught on the outer faces of the electric nets.

Experiment 1

The rates of skin and tail movements were greater than the rate of leg movements, and the latter was significantly greater than the rates of head and ear movements (table 2).

Table 2. Detransformed means and 95% confidence limits (C.L.) of skin, tail, leg, head and ear movement rates (per minute) of cattle. Within each experiment, means followed by the same letter are not significantly different at $P < 0.05$ (Tukey's test).

	skin	tail	leg	head	ear
			Movement type		
Experiment 1 (N=23)					
mean	6.9[a]	4.5[ab]	3.3[b]	0.9[c]	0.4[c]
95% C.L.	5.3–8.9	3.4–5.9	2.4–4.4	0.5–1.3	0.1–0.7
Experiment 2 (N=24)					
mean	1.8[a]	1.9[a]	1.1[a]	0.1[b]	0.1[b]
95% C.L.	1.3–2.4	1.4–2.5	0.7–1.5	0–0.4	0–0.3

Since not all skin movements were visible, it follows that skin ripples were probably the most frequent defensive movement. The rates of skin, tail, leg and head movements were generally correlated with each other, but none were significantly correlated with the rate of ear movements. Some of the correlations between pairs of variables may have existed because both were correlated with a third variable. To overcome this, partial correlation coefficients were calculated for each pair of transformed variables, excluding the rate of ear movements, with the values of other variables held constant. The only significant partial correlation coefficient was that between leg and tail movement rates ($r=0.47$, $n=23$, $P < 0.05$).

The relationship between the number of tsetse attracted to the cattle and the rate of defensive movements made by the cattle was examined by linear regression analysis of the rates of each of the movement types (y variables) on ox-catch (x-variable). There was no relationship between ox-catch and the total movement rate (Baylis & Mbwabi, 1995a), or ox-catch and the rates of tail, leg, head or ear movements. However, there was a significant, positive relationship between ox-catch and the rate of skin movements ($b=0.09$, $F_{1,21}=4.4$, $P < 0.05$).

The relationship between the rate of defensive movements made by the cattle and the feeding success of the tsetse was examined by linear regression analysis of the proportion of tsetse that engorged (y-variables) on the rates of each of the movement types (x-variables). There was a significant, negative relationship between the total movement rate of the cattle and the proportion of tsetse that

engorged (Baylis & Mbwabi, 1995a). There was a significant negative relationship between the rate of leg movements and the proportion of tsetse that engorged ($b=-0.15$, $F_{1,21}=10.7$, $P < 0.004$). Leg movement rate explained a greater percentage of the variance in the proportion of tsetse that engorged than did total movement rate (leg movement rate, 33.7%; total movement rate, 16.3%). There was also a negative relationship between head movement rate and the proportion of tsetse that engorged, although it did not reach significance ($F_{1,21}=3.8$, $P < 0.07$) and it explained only 15.4% of the variance in the proportion of tsetse that engorged. There were no relationships between the rates of skin, tail or ear movements and the proportion of tsetse that engorged.

The relationship between the number of tsetse attracted to the cattle and the feeding success of the flies was examined by linear regression analysis of the proportion of tsetse that engorged (y variable) on ox-catch (x-variable). There was no evidence for an effect of ox-catch ($b=0$, $F_{1,21}=0$, not significant). It is possible that the density of tsetse flies may affect feeding success in a manner independent of effects on host movement rate (for example, by direct competition among flies for feeding sites). This was examined by a multiple regression analysis which tested for an effect of ox-catch on the proportion of tsetse that engorged, after allowing for the effects of leg and head movement rates. Again, there was no effect of ox-catch on the proportion of tsetse that engorged ($b=0$, $F_{1,19}=0.5$, not significant).

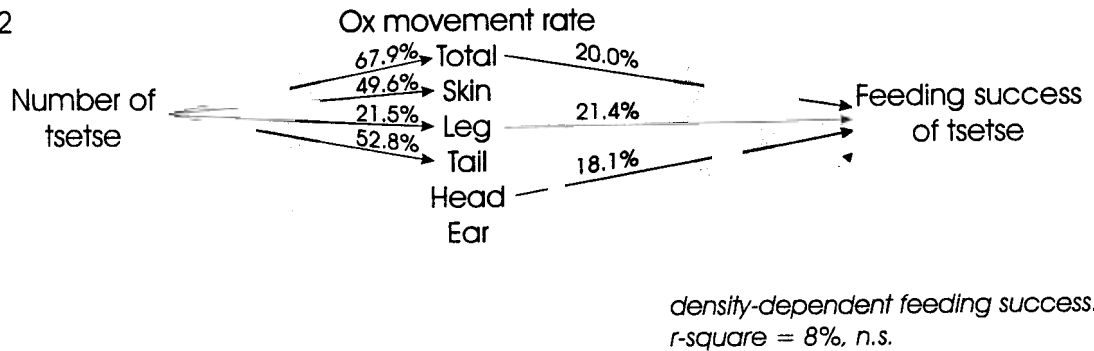These results are summarized in fig. 1A.
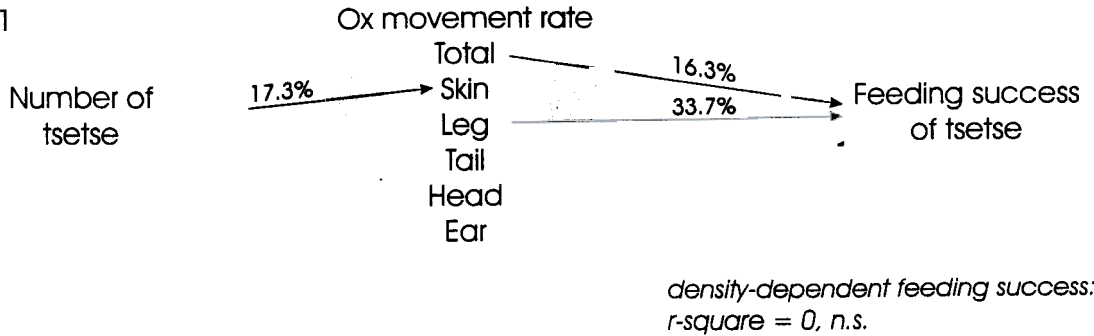
Fig. 1. Summary of the results of (A) experiment 1 and (B) experiment 2. Solid arrows indicate a significant effect of the variable to the left on the variable to the right. Numbers above arrows are the percentage of variance explained. The dotted arrow indicates the possible action of density-dependent feeding success.

Experiment 2

As in experiment 1, the rates of skin and tail movements were greater than the rate of leg movements, and the latter was significantly greater than the rates of head and ear movements (table 2). Partial correlation analysis revealed significant correlations between leg and tail movement rates ($r=0.42$, $n=24$, $P < 0.05$), skin and tail movement rates ($r=0.50$, $n=24$, $P < 0.05$), and leg and head movement rates ($r=0.70$, $n=24$, $P < 0.01$).

In contrast to experiment 1, there was a significant positive relationship between ox-catch and total movement rate (Baylis et al., 1994). Linear regression analysis of each of the movement rates on ox-catch revealed significant, positive relationships between ox-catch and skin movement rate ($b=0.19$, $F_{1,22}=21.7$, $P < 0.001$), ox-catch and tail movement rate ($b=0.23$, $F_{1,22}=24.7$, $P < 0.001$) and ox-catch and leg movement rate ($b=0.1$, $F_{1,22}=6.0$, $P < 0.05$).

There was a significant, negative relationship between the total movement rate of the cattle and the proportion of tsetse that engorged (Baylis et al., 1994). As in experiment 1, linear regression analysis revealed a significant negative relationship between the rate of leg movements and the proportion of tsetse engorged ($b=-0.13$, $F_{1,22}=6.0$, $P < 0.03$). In this experiment, leg movement rate explained approximately the same amount of the variance in the proportion of tsetse that engorged as total movement rate (leg movement rate, 21.4%; total movement rate, 20.0%). There was also a significant negative relationship between head movement rate and the proportion of tsetse that engorged ($F_{1,22}=4.85$, $P < 0.04$) and it accounted for 18.1% of the variance in the proportion of tsetse that engorged. There were no relationships between the rates of skin, tail or ear movements and the proportion of tsetse that engorged.

The relationship between the number of tsetse attracted to the cattle and the proportion of tsetse that engorged was negative ($b=-0.018$), but not significant ($F_{1,22}=2.0$). As in experiment 1, there was no effect of ox-catch on the proportion of tsetse that engorged, after allowing for the effects of leg and head movements ($b=-0.006$, $F_{1,20}=0.2$, not significant).

These results are summarized in fig. 1B.

Nutritional state of tsetse

Host defensive behaviour might, by disturbing feeding flies, act to reduce the mean size of bloodmeals taken by tsetse. An attempt to estimate bloodmeal size was made by measuring the haematin contents of the fed male G. pallidipes in experiment 1. However, haematin contents of recently fed tsetse are related in a quadratic fashion to the packed cell volume of the cow or heifer from which the bloodmeal was taken (Baylis & Mbwabi, 1995b). Therefore, for each fed tsetse, a better estimate of bloodmeal size is the difference between the observed haematin content and that predicted from the packed cell volume of its host. This difference is the residual from the regression analysis of haematin content on PCV^2. Residuals were obtained for each fed male G. pallidipes and means were calculated for each cow or heifer. There were no significant correlations between the mean residual for each animal and any of the individual movement rates or total movement rate. There was a significant correlation between the mean residual and the body temperature of the cow or heifer (see Baylis & Mbwabi, 1995b).

Previous research has demonstrated that male G. pallidipes with lower fat contents are more likely to feed on a cow or heifer than are male flies with higher fat contents (i.e. hungriness is inversely related to fat content; Baylis & Nambiro, 1993). Given that defensive movements by cattle, especially leg movements, decrease the feeding success of G. pallidipes there are two likely scenarios for the effects of host defensive behaviour on the fat contents of the flies that feed: (i) flies of different fat contents respond to the level of defensive behaviour by equal amounts; (ii) flies with lower fat contents (i.e. hungrier flies) are deterred less by high levels of defensive behaviour than are flies with higher fat contents. Under the first scenario, the fat contents of fed flies would not change with increase in the level of host defensive behaviour. Under the second scenario, the fat contents of fed flies would decrease with increase in the level of host defensive behaviour. In experiment 1, there was significant day-to-day variation in the mean fat content of the male tsetse that were caught around the cattle (Baylis & Mbwabi, 1995a). When the mean fat content of the male tsetse that fed on each cow or heifer is expressed as a fraction of the mean fat content of all male tsetse that were caught around each animal (giving a value that expresses, inversely, the extent to which the tsetse that fed are a hungry sub-sample of the tsetse that approached; hereafter called the relative fat content), there is a significant relationship with leg movement rate of the cow or heifer (fig. 2). In general, the relative fat content of engorged tsetse decreases as leg movement rate increases; in other words, as the rate of leg movements increases, the tsetse that feed are a hungrier sub-sample of the tsetse that approach. The relative fat content of fed flies also tended to decrease with total, skin, and tail movement rates, but the relationships were not significant.

As the leg movement rate of cattle increases, both the feeding success of tsetse and the relative fat contents of the tsetse that feed tend to decrease – the feeding population
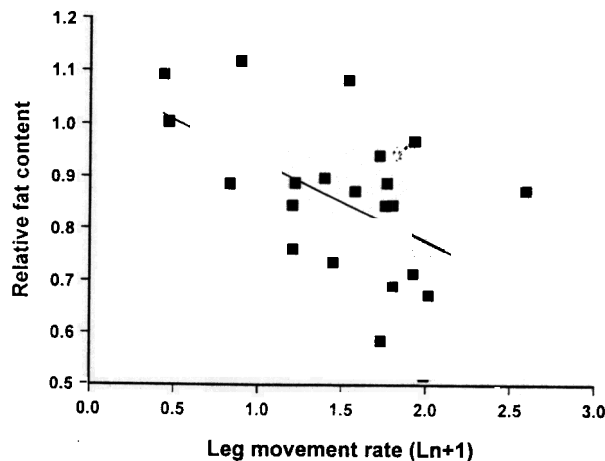

Fig. 2. Effect of the rate of leg movements (per minute) of cattle on the relative fat content of male Glossina pallidipes that fed on the cattle. Relative fat content is the mean fat content of the fed male tsetse expressed as a fraction of the mean fat content of the male tsetse that approached the cattle, and indicates, inversely, to what extent the fed tsetse are a hungry sub-sample of the tsetse that approached. The regression line $y = 1.09 - 0.155x$ is shown ($F_{1,20}=7.26$, $P < 0.02$).
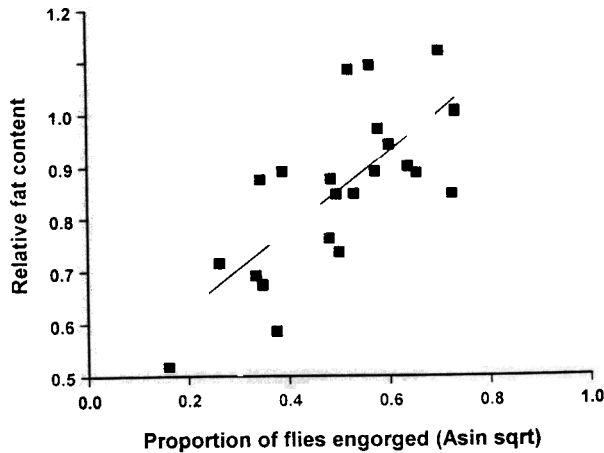
Fig. 3. Relationship between the proportion of *Glossina pallidipes* that fed on cattle and the relative fat content of the fed male tsetse. Relative fat content is the mean fat content of the fed male tsetse expressed as a fraction of the mean fat content of the male tsetse that approached the cattle, and indicates, inversely, to what extent the fed tsetse are a hungry sub-sample of the tsetse that approached. The regression line $y = 0.476 + 0.753x$ is shown ($F_{1,26} = 23.09$, $P < 0.001$).

is smaller and hungrier. A relationship between feeding success and hungriness might therefore be expected, and this is indeed the case (fig. 3).

Discussion

When a tsetse fly approaches a host, the probability that it will take a bloodmeal will be determined by many factors. Among these, two of the most important are its own hungriness and the opportunity presented by the level of defensive behaviour of the host. In theory, these two factors can act independently of each other: for example, if a host is twice as active, the probabilities of feeding for both more- and less-hungry tsetse may be halved. In fact, results presented here suggest that the two factors do not behave independently; rather, it appears that if a host is more active, hungrier flies are deterred to a lesser extent than are other flies. This finding supports the model of Randolph *et al.* (1992), and models II and III of Hargrove & Williams (1995), in which the feeding strategy of tsetse is based on a balance between conflicting risks of mortality: the risk of starvation if a fly does not feed, and the risk of death (from predation or host defensive behaviour) if a fly does feed. In this scenario, if a tsetse has a low fat content with a consequent high risk of starvation should it not feed, then a higher risk of death from host defensive behaviour is acceptable in the attempt to obtain a bloodmeal.

A third factor that might affect the probability of a tsetse obtaining a bloodmeal is the number of other tsetse (or blood sucking insects) also attempting to feed. Results presented here suggest a possible reason why there is only weak evidence for such density-dependence for *G. pallidipes*. It appears that cattle respond most strongly to attack by *G. pallidipes* with skin ripples, yet these movements do not affect the feeding success of the flies. Rather, leg movements affect feeding success, but tsetse number has relatively little or no effect on their rate. Nevertheless, density-dependent

feeding success by *G. pallidipes* has been reported: Vale (1977) found significant, weakly negative relationships between tsetse number and tsetse feeding success in four out of eight studies. Here, in one experiment there was a significant effect of tsetse number on the rate of leg movements, and this, combined with the effect of leg movements on feeding success, should have resulted in density-dependent feeding success. In fact, there was a negative relationship between tsetse number and the proportion that engorged, which is indicative of density-dependent feeding success, but it was not significant. This pattern (a negative relationship between tsetse density and feeding success which is, nevertheless, not significant) is a common finding in studies of tsetse feeding success (Vale, 1977; Torr, 1994) suggesting that density-dependence exists, but is usually too weak to detect with current methods. A positive relationship between tsetse density and feeding success (which was not significant) has been reported in only one study (Vale, 1977).

It is possible that the density of tsetse in the experiments described here was below a threshold at which density-dependence might be observed. The catches around cattle peaked at about 200 in 120–130 minutes; assuming that the electric net arrangement catches five-ninths of all tsetse attracted, this suggests a maximum density of *G. pallidipes* at an ox of about 3 per minute. Vale (1977) presented evidence for density-dependence, with maximum densities of the order of 1000 in 3 hours, or 5.5 per minute. In contrast, Torr (1994) found no evidence for density-dependence, despite maximum densities of about 15 per minute (based on maximum catches of 800 tsetse in 90 minutes, and electric nets covering 35% of the circle around the pen). There is thus no clear pattern between tsetse density and the ability to demonstrate density-dependent feeding success.

The measure of feeding success used here, proportion-engorged, gives lower values than that used by Vale (1977). Vale's method is based entirely on flies caught on the inner faces of the electric nets which, in theory, should be a good indication of the actual feeding success. In fact, significant numbers of engorged tsetse are usually caught on the outer faces of the electric nets. Since it is unclear whether unfed tsetse also circle the nets, a measure that makes no assumptions about the flight behaviour of tsetse, such as proportion-engorged, may be preferable as a measure of feeding success. However, based on fat contents, Baylis & Nambiro (1993) presented evidence that the degree of mixing of unfed *G. pallidipes* on the inner and outer faces of the electric nets is, at most, small. If so, the best true measure of feeding success may be to follow Vale (1977), but include *all* fed tsetse as part of the inside catch (i.e. feeding success = (fed_{inside} + $fed_{outside}$)/($total_{inside}$ + $fed_{outside}$)). Proportion-engorged, defined earlier as (fed_{inside} + $fed_{outside}$)/($total_{inside}$ + $total_{outside}$), is highly correlated with this measure of feeding success ($r > 0.95$ for both experiments described here), suggesting that the findings presented here retain validity. The above formula gives mean estimates of feeding success of 39–40% for the data presented here, comparable to those given by Vale (1977).

Baylis & Mbwabi (1995a) reported that the number of *G. pallidipes* attracted to cattle did not affect the total rate of defensive movements made by the cattle. In contrast, using a similar experimental design Baylis *et al.* (1994) found a strong positive relationship between the two variables.

The more detailed analysis presented here reveals that the results of the two experiments are not entirely contradictory. In both experiments there was a significant effect of tsetse number on the rate of skin movements; in the second experiment there were also significant effects of tsetse number on the rates of tail and leg movements. Since skin, tail and leg movements comprise the vast majority of defensive movements, in experiment 2 there was a significant effect of tsetse number on the total rate of defensive movements.

Both studies report that the feeding success of tsetse is affected by the rate of defensive movements of the cows and heifers. Surprisingly, although leg movements accounted for only about 20% of observed defensive movements, in both experiments the rate of leg movements explained more of the variance in feeding success than did total movement rate, and the rates of the (more numerous) skin and tail movements had no effect. These results are particularly interesting in light of the findings of Thomson (1987), who reported that the lower leg is the preferred landing site, and presumably feeding site, of G. pallidipes on cattle. The belly and back are reported to be the preferred landing sites of a second tsetse species, G. m. morsitans. This raises the intriguing possibility that the relationships between tsetse number, ox movement rate, and tsetse feeding success may differ between the two species.

The results presented here emphasize the importance of the rate of host defensive movements in determining the feeding success of tsetse. Since the total (and leg) movement rates were three times greater in experiment 1 than experiment 2, a lower feeding success in experiment 1 would be predicted, but no difference in feeding success was found. Explanations for the failure of this prediction, which is based on clear patterns observed within experiments, may include possible effects of site or season. More specifically, however, it illustrates how much is still unknown about the factors that determine the feeding success of tsetse.

Acknowledgements

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