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The feeding success of tsetse flies, *Glossina pallidipes* (Diptera: Glossinidae), on oxen treated with pyrethroid pour-ons at Galana Ranch, Kenya

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Abstract

An experiment was conducted at Galana Ranch, Kenya, which examined, under natural conditions, whether treatment of oxen with insecticidal pour-ons affects the success with which tsetse flies (*Glossina pallidipes* Austen) feed on them. An incomplete ring of electric nets was used to sample *G. pallidipes* approaching and departing from oxen that were either untreated, or treated 6-12 days previously with pour-ons containing deltamethrin or cypermethrin. Eight animals of each treatment were used. There was no evidence suggesting that pour-on application affected the number of *G. pallidipes* attracted to oxen. A positive relationship was observed between the number of *G. pallidipes* that approached an ox and the frequency with which it made anti-fly movements. There was also a significant, negative relationship between the rate of anti-fly movements and the proportion of *G. pallidipes* that fed on the oxen. However, there was no effect of pour-on application on either the rate of anti-fly movement or on the proportion of tsetse that fed. It is concluded that even recent application of deltamethrin or cypermethrin pour-ons to an ox does not affect the ability of *G. pallidipes* to feed; and that the feeding success of *G. pallidipes* is density dependent because when more tsetse approach an ox its rate of anti-fly movements increases and the proportion of tsetse that feed decreases.

Introduction

Several recent studies in Africa have shown that regular treatment of large numbers of oxen (>400) with formulations of photostable pyrethroids (pour-ons) can significantly reduce the incidence of trypanosomiasis in the animals (Chizyuka & Luguru, 1986; Löhr *et al.*, 1991; Stevenson *et al.*, 1991; Thomson *et al.*, 1991; Bauer *et al.*, 1992a; Thomson & Wilson, 1992a, 1992b). This is probably due to control of the tsetse vector (*Glossina* spp.) but an alternative explanation may be that pour-on application affects the ability of tsetse to probe and feed, and hence infect the animals. Distinction between these possibilities is important. If the ability of the vectors to feed is reduced but they are not controlled, a break in the application of the pour-on may lead to a sudden increase in the incidence of infection. If the vectors are controlled but their ability to feed is not affected, the incidence of infection may be high when oxen treated with pour-on first come into contact with large numbers of tsetse, unless the oxen are also protected with prophylactic drugs, or the tsetse are initially controlled by some other means. This paper addresses the question of whether pour-ons affect the ability of tsetse to feed on cattle.

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It has been reported that tsetse will feed on oxen only recently treated with deltamethrin spray (Thomson, 1987; Thomson *et al.*, 1991). However, no data were presented comparing the feeding success of the tsetse on treated and untreated oxen, and thus the existence of an effect of pour-on cannot be discounted. Bauer *et al.* (1992b) released teneral tsetse into fly-chambers containing oxen that were either untreated, or treated with a deltamethrin pour-on, and found that pour-on application reduced feeding success even six weeks after treatment. The reduction was attributed to the paralysis of tsetse that landed repeatedly on the treated animal before having an opportunity to feed. No such effect was observed when oxen were treated with a flumethrin pour-on (Bauer. *et al.*, 1989).

Here, we describe an experiment, conducted under natural conditions at Galana Ranch, south-eastern Kenya, to determine whether treatment of oxen with the pour-ons Spot On* or Ectopor** affects the success with which *G. pallidipes* Austen feed on them.

Materials and methods

Galana Ranch is a 6000 km^2 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 experimental site was near the south-eastern edge of the ranch, at the base of Dakabuku hill. It consisted of a circular clearing of approximately 15 m diameter with a track passing on one side. Two thornbush corrals (for housing oxen at night) were constructed 500 m from the experimental site, one in each direction along the track. This allowed two groups of oxen to be kept in the vicinity of the experimental site at any one time.

The oxen used in the experiment were white-coloured Orma Boran cows or heifers, selected from the Orma Breeding Herd of Galana Ranch. The oxen were not maintained under prophylaxis against trypanosomiasis, and only animals found to be uninfected by examination of wet blood smears were selected.

Groups of two to four animals were walked approximately 15 km from the main herd to the vicinity of the experimental site. Groups were allocated to one of three treatments: untreated; treated with Spot On; or treated with Ectopor. To minimize the risk of contamination of pour-ons among oxen the following precautions were taken: oxen treated with Spot On and those treated with Ectopor shared one corral, but never at the same time, and they were housed in separate parts of the corral; the second corral was kept for untreated animals only; oxen from the different groups grazed in different areas; untreated animals watered in a different place from the treated animals; different herdsmen looked after the untreated and the treated animals; the herdsmen looking after the treated animals washed themselves and their clothes thoroughly when switching from a group treated with one pour-on to a group treated with the other; technical staff wore colour-coded uniforms according to the treatment of the ox used that day; and before being returned to the main herd, groups of oxen were washed using detergent.

*Deltamethrin 1% w/v (Coopers, Zimbabwe)
**Cypermethrin high cis 2% w/v (Ciba-Geigy Animal Health)

Treatment of oxen

At the corral, oxen were treated with the two pour-ons according to the manufacturers' instructions. Spot On was applied in a line along each side of the animal, at a dose of 1 ml/10 kg body weight, using an automatic syringe fitted with a T-shaped applicator. Ectopor was squirted from syringes as one line along each side of the animal, and two lines along the back, at the same overall dose of 1 ml/10 kg body weight. Oxen were used in the experiment 6-12 days after treatment with pour-on. This time period was chosen to allow the chemicals time to disperse over the animal's body, and to be within the treatment interval recommended by the manufacturers (Spot On, 4 weekly; Ectopor 2-4 weekly).

Experimental design

The experiment was conducted over 26 days during a 46 day period between May and July 1993. Only one animal was used per day. Each day at 15.30 h an ox was placed in a pen constructed from widely-spaced metal bars, of total size 2.0×0.7×1.5 m (l×w×h), which was surrounded by an incomplete ring of electric nets (Vale, 1974). Each net comprised 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 ox. The electric nets were operated from 16.00-18.10 h. 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. At the end of each experiment, the tsetse were collected, sorted and counted. Tsetse were classed as recently fed if red blood was visible through the wall of the abdomen.

Each ox was watched from a distance of 30 m using binoculars, and anti-fly movements were recorded. The movements included in this category were tail swishing, leg kicking, skin rippling, head swinging or shaking, and ear flapping. It was not feasible to observe the oxen for the 130 minutes that the experiment was operated each day, and a 20 minute period only, from 17.30-17.50 h, was selected. After the experiment, the body temperature of the ox was measured. Blood samples were taken for determination of packed cell volume, and for examination for trypanosomes in the whole blood and buffy coat. One ox (which was treated with Spot On) was found to have become infected with *Trypanosoma vivax*. This is unlikely to have affected its attractiveness to tsetse, or their feeding success (Baylis & Mbwabi, in press).

There were three identical metal pens, one for each treatment. The two unused pens were kept a few metres from the experimental site.

Since only two groups of oxen were in the vicinity of the experimental site at any one time, it was not possible to select oxen randomly from the three treatments for use in the experiment. Instead, animals were used group by group. The order in which animals were used was as follows: 4×U, 4×SO, 2×U, 4×E, 2×U, 4×SO, 2×U, 4×E, where U=Untreated, SO=Spot On and E=Ectopor. These animals were all different individuals.

To provide an estimate of daily variation in tsetse density, three Epsilon traps (Hargrove & Langley, 1990),

baited with acetone (500 mg/h) were set from 16.00-18.10 h at distances of about 200 m from the experimental site.

Calculation of parameters

Four parameters were calculated for each ox: 1. Ox-catch: the total number of *G. pallidipes* caught on both sides of the electric nets. 2. Trap-catch: the mean number of *G. pallidipes* per trap. 3. Movement rate: the mean number of anti-fly movements per minute. 4. Proportion engorged: the proportion of the ox-catch classified as fed. The proportion engorged was calculated this way, rather than as a proportion of the number caught on the inside of the electric nets, because it is known that some fed tsetse, and possibly unfed tsetse, will circle an electric net before being caught (Baylis & Nambiro, 1993c).

Control

To find out whether fed tsetse were caught in the absence of an ox, on one day the experiment was run with a 2×1 m black target in the crush. The target was baited with acetone (500 mg/h), and a polythene sachet containing 4 ml of a 8:4:1 mixture of 4-methylphenol: 1-octen-3-ol: 3-propylphenol (Baylis & Nambiro, 1993a). There was not a single recently fed tsetse out of the 38 caught.

Data analysis

During the experiment there was considerable variation in tsetse numbers, and ox-catches of *G. pallidipes* ranged almost seventy-fold. Data from the day with the lowest ox-catch (22nd day, 4 tsetse) were not included in any analyses because of the inaccuracy of proportions (such as the proportion of tsetse that engorged) based on small sample sizes. The largest ox-catch of *G. pallidipes* (1st day, 276 tsetse) was more than twice that of the second largest catch. Data for this day were in line with other data and are shown on the figures, but were found to have a very strong effect on all analyses, and were therefore excluded. Ox-catches of *G. pallidipes* on the remaining 24 days ranged from 14 to 120, with a mean ± S.D. of 58 ± 33. The treatment sample sizes used in analyses are: Untreated, 8; Spot On, 8; Ectopor, 8.

Parameters were transformed prior to statistical analysis (Sokal & Rohlf, 1981). The proportion of tsetse that engorged was arcsine transformed; the rate of anti-fly movements was logarithmically transformed; the catch of *G. pallidipes* around each ox, and the mean of the three trap catches, had Poisson distributions and were therefore square-root transformed. Means, and means ± 95% confidence intervals, were detransformed prior to presentation (Zar, 1984). All analyses were performed using the statistical package Minitab™.

Results

Biological parameters of oxen

The oxen of each treatment did not differ significantly in weight (means in kg: Untreated, 289; Spot On, 270; Ectopor, 255; $F_{2,23}=1.98$ n.s.), packed cell volume (means: Untreated, 28.3; Spot On, 28.5; Ectopor, 27.8; $F_{2,23}=0.06$ n.s.) or body temperature (means in °C: Untreated, 39.0; Spot On, 39.1; Ectopor, 39.0; $F_{2,23}=0.11$ n.s.).

Trap-catch and ox-catch

Over the time period that the experiment was conducted there was a general decline in trap-catch, followed by a sharp increase during the final few days (fig. 1A). This trend, combined with the non-random order in which oxen from the three treatments were used, made the treatments

Table 1. Detransformed means and 95% confidence limits (C.L.) of trap-catch, ox-catch, the ratio of ox-catch to trap-catch, movement rate and the proportion of *Glossina pallidipes* that fed on oxen that were either untreated, treated with Spot On or treated with Ectopor. The following definitions were used: *ox-catch*, the total number of *Glossina pallidipes* caught on the electric nets; *trap-catch*, the mean number of *Glossina pallidipes* per trap; *movement rate*, the number of anti-fly movements per minute; *proportion engorged*, the proportion of the ox-catch classified as fed.

Parameter	Treatment of cattle			Effect of treatment
	Untreated (N=8)	Spot On (N=8)	Ectopor (N=8)	
Trap-catch				
mean	28.9	9.6	14.2	$F_{2,21}=4.3^{*}$
C.L.	17.7-42.7	3.6-18.3	6.7-24.3	
Ox-catch				
mean	70.5	38.7	53.2	$F_{2,21}=2.2$ n.s.
C.L.	47.1-98.6	21.9-60.2	33.1-77.9	
Ratio of ox-catch : trap-catch				
mean	2.7	5.5	3.9	$F_{2,21}$ .4 n.s.
C.L.	1.1-5	3.0-8.6	1.9-6.7	
Movement rate				
mean	5.4	4.5	5.6	$F_{2,20}=0.4$ n.s.
		3.0-6.	3.9-8.	
Proportion engorged[2]				
mean	0.26	0.20	0.17	$F_{2,20}=1.6$ n.s.
C.L.	0.19-0.35	0.13-0.28	0.11-0.24	

[1]Means are adjusted means from the ANCOVA with ox-catch as a covariate. Effect of covariate, $F_{1,20}=33.2^{***}$; [2]Means are adjusted means from the ANCOVA with movement rate as a covariate. Effect of covariate, $F_{1,20}=6.4^{*}$; n.s., not significant; $^{*}P < 0.05$; $^{***}P < 0.001$.

differ significantly in trap-catch on the days that they were conducted (table 1).

A similar pattern was observed for ox-catch, although the trend was less clear (fig. 1B). As before, because of the non-random order in which oxen from the three treatments were used, the mean ox-catch differed among treatments, although not significantly (table 1).

The ratio of ox-catch to trap-catch should be altered if pour-ons affect the attractiveness of oxen to tseste. The mean ratios were greater for treated than untreated oxen (table 1), suggesting an increase in attractiveness, but the difference was not significant. The effect might instead be attributed to changes in the relationship between ox-catch and trap-catch at lower and higher numbers of flies (fig. 2). For higher numbers of tsetse, ox-catch appears to increase approximately linearly with trap-catch. However, at lower numbers this relationship appears to break down and fairly high ox-catches (for all three groups of oxen) may be associated with low trap-catches. It is suggested here that, because a greater proportion of treated oxen were examined on days on which there were low trap-catches, there was a greater proportion of treated oxen with higher ratios of ox-catch to trap-catch.

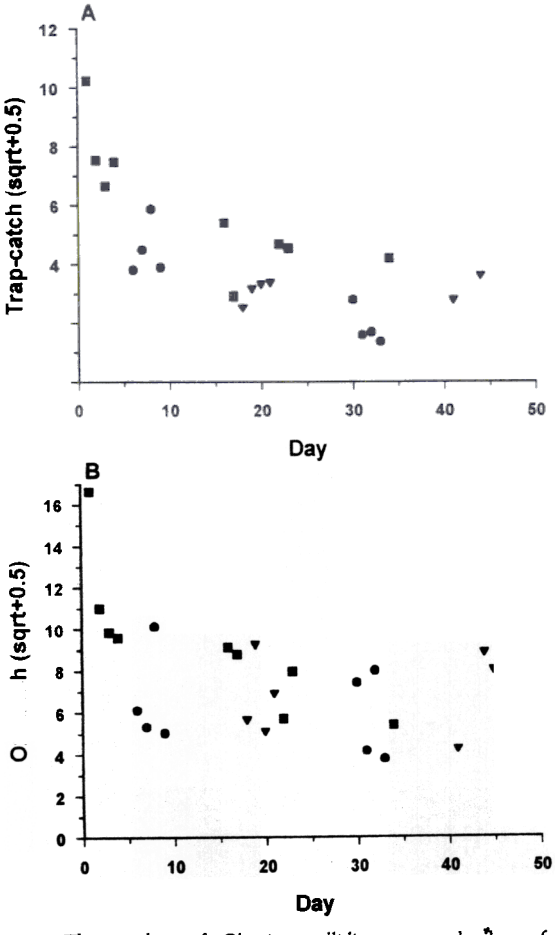

Fig. 1. The catches of *Glossina pallidipes* on each day of the experiment in three traps (A, mean per trap) and around oxen (B). Symbols refer to the treatment of the ox used that day: square, untreated; circle, treated with Spot On; triangle, treated with Ectopor.

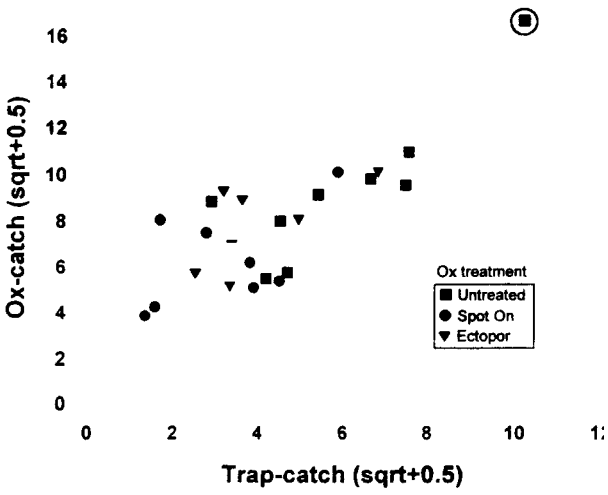

Fig. 2. The relationship between trap-catch and ox-catch on each day of the experiment. Oxen were either untreated, or treated with pour-ons containing deltamethrin (Spot On) or cypermethrin (Ectopor). The point for the first day of the experiment is shown (circled).

Movement rate

Movement rate ranged from 0.6 to 20.7 movements per minute. It increased with the ox-catch of *G. pallidipes* (fig. 3; regression, $F_{1,22}=46.4$, $P < 0.001$). The effect of pour-on treatment on movement rate was then examined by ANCOVA with ox-catch as a covariate. No effect of treatment was found (table 1).

Proportion of tsetse that engorged

A total of 361 fed *G. pallidipes* were caught during the experiment. Of these, 60 (16.6%) were caught on the outside

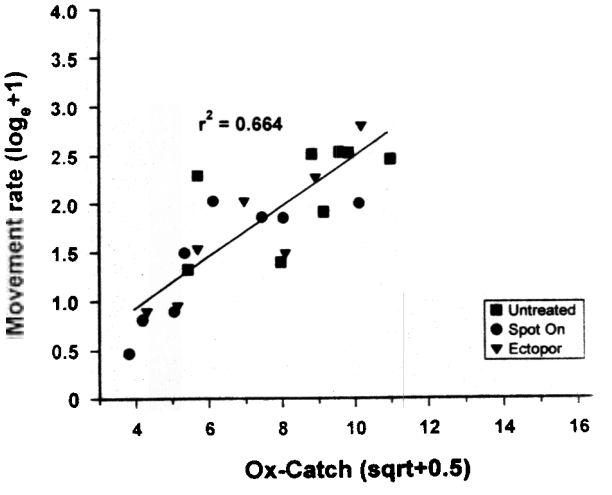

Fig. 3. The effect of the number of *Glossina pallidipes* caught around oxen on the rate (per minute) at which the oxen made anti-movements. Each point represents a separate ox. Oxen were either untreated, or treated with pour-ons containing deltamethrin (Spot On) or cypermethrin (Ectopor). The regression line $y=0.26x-0$ is shown. The point for the first day of the experiment is shown (circled) but was not included in analyses.

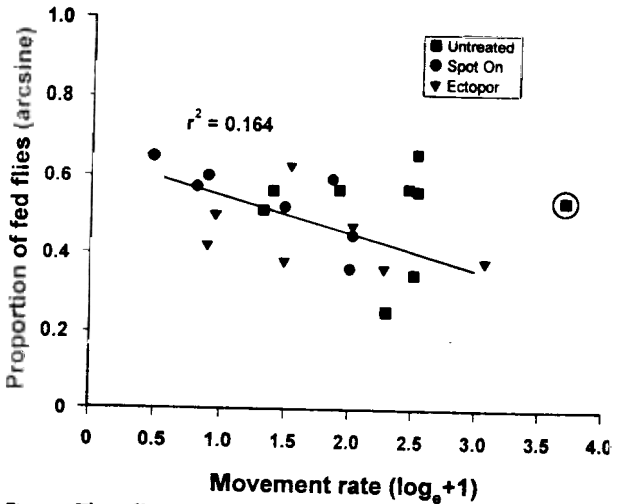

Fig. 4. The effect of the rate (per minute) at which oxen made anti-fly movements on the proportion of *Glossina pallidipes* that engorged. Each point represents a separate ox. Oxen were either untreated, or treated with pour-ons containing deltamethrin (Spot On) or cypermethrin (Ectopor). The regression line $y=-0.09x+0.64$ is shown. The point for the first day of the experiment is shown (circled) but was not included in analyses.

of the electric nets. This is similar to the 15.6% of fed tsetse caught on the outside of electric nets around oxen reported by Baylis & Nambiro (1993c).

The proportion of *G. pallidipes* that engorged ranged from 0.04 to 0.43. Its level might be affected by many parameters, including ox-catch, movement rate, and the weight, packed cell volume and body temperature of the ox (Rossignol & Shieh, 1993). The proportion of tsetse that engorged was subjected to multiple regression analysis with these five parameters as independent variables which were eliminated backwards (i.e. variables were removed one by one, the least significant first, until only significant variables remained). Of the five parameters listed above, only movement rate had a significant effect on the proportion of tsetse that engorged (fig. 4; regression, $F_{1,22}=5.52$, $P < 0.03$). Any effect of ox-catch might have been reduced because of its significant correlation with movement rate. Therefore, the data were reanalysed with movement rate excluded from the model but ox-catch again did not have a significant effect.

The effect of pour-on treatment on the proportion of tsetse that engorged was examined by ANCOVA, with movement rate as a covariate. The mean proportion of engorged tsetse was greater on untreated oxen than on those treated with pour-on, but the differences were small and not significant (table 1).

Discussion

Pour-ons applied to oxen may directly affect their susceptibility to attack by tsetse in at least three ways; they may affect the number of tsetse attracted (long-distance); after attraction, the proportion of tsetse that land (short-distance); or, after landing, the proportion of tsetse that probe or feed (post-contact).

In our experiment, long-distance effects were examined by comparing ox-catch with trap-catch. No significant effects were found, the differences in the ratios of ox-catch to trap-catch perhaps being attributable to changes in the relationship between the two variables at lower or higher numbers of tsetse, and the tendency for treated oxen to have been examined on days with lower numbers of tsetse. Long-distance effects are not expected because most components of pour-on formulations are largely non-volatile.

The experimental design used could not distinguish between short-distance and post-contact effects, which were examined by measuring the proportion of tsetse that engorged. After allowing for differences in the activity levels of the oxen, there was no effect of pour-on application on the proportion of *G. pallidipes* that engorged, suggesting that neither short-distance nor post-contact effects occur (unless both occur, but in opposite directions). Our results support those of Thomson (1987) who observed *G. pallidipes* feeding on oxen treated with deltamethrin spray, and Bauer *et al.* (1989) who reported no effect of a flumethrin pour-on on the proportion of *G. palpalis gambiensis* Vanderplank that fed on oxen. They disagree with the results of Bauer *et al.* (1992b) who released teneral *G. palpalis gambiensis* into fly chambers containing oxen that were either untreated, or treated with deltamethrin pour-on. These workers found that the proportion of tsetse that fed in two hours was approximately 30% lower on oxen treated 1-10 days earlier than on untreated oxen, and there was evidence of a lower tsetse feeding success up to 41 days post-treatment, the effect being attributed to post-contact paralysis of tsetse before finding an opportunity to feed. Such an effect could have been, but was not, detected with our experimental design as a reduction in the proportion of tsetse that engorged. There are several possible reasons for the difference in findings. One is the confinement of tsetse in the fly chamber used by Bauer *et al.* (1992b) since an aerosol of certain pour-on components may knock down some tsetse before contact (P.A. Langley, pers. comm.). A second reason might be the young age of the tsetse used by Bauer *et al.* (1992b) since teneral tsetse, with their softer cuticle, are more susceptible to pyrethroids than older tsetse (P.A. Langley, pers. comm.).

The proportion of engorged tsetse was calculated as the proportion of all *G. pallidipes* caught around an ox that had fed. However, the electric nets killed tsetse both approaching and departing from the oxen and approaching tsetse had not had an opportunity to feed. Therefore, the proportion of tsetse that engorged does not accurately reflect the success with which they obtained blood meals. In the design used here, the electric nets covered one-third of the circumference of a ring around the ox. It follows, therefore, that of all *G. pallidipes* caught, only two-fifths should have been departing. A better estimate of feeding success is therefore given by dividing the proportion of engorged tsetse by two-fifths. This gives estimates of feeding success of *G. pallidipes* on oxen of the three treatments as follows: untreated, 0.65; Spot On, 0.50; Ectopor, 0.43. These estimates are slightly higher than the value of 0.36 for uninfected oxen at Galana Ranch reported by Baylis & Nambiro (1993b), which may reflect differences in either the season or the site at which the experiments were conducted.

Considering data from several experiments, Vale (1977) reported that the feeding success of *G. pallidipes* was generally lower when larger numbers approached an ox. Also, when the number of tsetse attracted to an ox was increased 4.5 times using odour attractants, the ox became three times more active, and the feeding success of the tsetse

decreased. These findings suggest that the feeding success of tsetse is density dependent (Rogers & Randolph, 1984; 1985). The work presented here provides further evidence of density dependence. The proportion of tsetse that engorged declined significantly with increase in the movement rate of the oxen, while movement rate itself was strongly and positively correlated with the number of tsetse approaching the oxen. The density dependence is weak, however: the slope of the regression line of the proportion of engorged tsetse on ox-catch was negative ($b = -0.0183$), but not significant.

Previous studies of the effect of pour-on application on the feeding success of tsetse have used only two or three oxen (Thomson, 1987; Bauer *et al.*, 1989, 1992b). In the work presented here there was an 11-fold range in the (untransformed) proportion of *G. pallidipes* that fed on the oxen, with movement rate accounting for only 16.4% of the variation (fig. 4). The sources of the remaining variation might include both ox and day effects. The amount of variation attributable to ox-effects might be estimated by measuring the feeding success of tsetse on the same oxen for several days each. Nonetheless, it is clear that there should be considerable replication of host animals and days in future studies on the feeding success of tsetse if such variation is to be overcome.

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