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Is there safety in numbers? The effect of cattle herding on biting risk from tsetse flies

S. J. TORR[1], A. PRIOR[1], P. J. WILSON[2] and S. SCHOFIELD[2]
[1]Natural Resources Institute, University of Greenwich, Greenwich, U.K. and [2]Department of Biology, Trent University, Peterborough, Ontario, Canada

Abstract. In sub-Saharan Africa, tsetse (*Glossina* spp.) transmit species of *Trypanosoma* which threaten 45–50 million cattle with trypanosomiasis. These livestock are subject to various herding practices which may affect biting rates on individual cattle and hence the probability of infection. In Zimbabwe, studies were made of the effect of herd size and composition on individual biting rates by capturing tsetse as they approached and departed from groups of one to 12 cattle. Flies were captured using a ring of electrocuting nets and bloodmeals were analysed using DNA markers to identify which individual cattle were bitten. Increasing the size of a herd from one to 12 adults increased the mean number of tsetse visiting the herd four-fold and the mean feeding probability from 54% to 71%; the increased probability with larger herds was probably a result of fewer flies per host, which, in turn, reduced the hosts' defensive behaviour. For adults and juveniles in groups of four to eight cattle, $>$ 89% of bloodmeals were from the adults, even when these comprised just 13% of the herd. For groups comprising two oxen, four cows/heifers and two calves, a grouping that reflects the typical composition of communal herds in Zimbabwe, ~ 80% of bloodmeals were from the oxen. Simple models of entomological inoculation rates suggest that cattle herding practices may reduce individual trypanosomiasis risk by up to 90%. These results have several epidemiological and practical implications. First, the gregarious nature of hosts needs to be considered in estimating entomological inoculation rates. Secondly, heterogeneities in biting rates on different cattle may help to explain why disease prevalence is frequently lower in younger/smaller cattle. Thirdly, the cost and effectiveness of tsetse control using insecticide-treated cattle may be improved by treating older/larger hosts within a herd. In general, the patterns observed with tsetse appear to apply to other genera of cattle-feeding Diptera (*Stomoxys*, *Anopheles*, Tabanidae) and thus may be important for the development of strategies for controlling other diseases affecting livestock.

Key words. *Glossina*, cattle, feeding behaviour, microsatellite DNA, tsetse fly, Zimbabwe.

Introduction

Many animals are gregarious, a major benefit of which is thought to be the protection from predators provided by being close to other con-specifics (Hamilton, 1971), dilution effects (Foster & Treherne, 1981) or improved anti-predator vigilance (Bednekoff & Lima, 1998). Much of the work on this topic has been concerned with classical predator−prey relationships, such as lions hunting cattle (Hamilton, 1971) and hawks attacking pigeons (Kenward, 1978). However, Hamilton's (1971) seminal paper on the 'selfish herd' also recognized that similar arguments might be applied to flies feeding on herds of ungulates. Several studies have shown that caribou (Bergerund, 1974), feral horses (Rutberg, 1987) and domestic cattle

Correspondence: Stephen J. Torr, Natural Resources Institute, Central Avenue, Chatham, Kent ME4 4TB, U.K. Tel.: + 44 1634 883304; Fax: + 44 1634 883379; E-mail: s.torr@greenwich.ac.uk

(Schmidtmann & Valla, 1982) congregate when the densities of biting fly are high and these responses may reduce individual fly load and hence blood loss, irritation and infection with fly-borne parasites.

For livestock, the size, composition and geometry of groups is controlled largely by the owner. Consequently, management practices might impact on the epidemiology and control of insect-borne diseases. One complex of diseases for which this may be important is African animal trypanosomiasis; these diseases, caused by *Trypanosoma* species transmitted by tsetse flies (*Glossina* spp., Diptera: Glossinidae), threaten the health and productivity of 45–50 million cattle (Shaw, 2004). Over the ~ 10 million km^2 of sub-Saharan Africa that tsetse infest, there are a wide variety of cattle management practices. These range between small-scale dairy producers who keep solitary animals in a pen, mixed crop/livestock farmers who keep medium-sized groups of 10–20 cattle and small stock together (Hargrove *et al*., 2003) and traditional pastoralists and commercial ranchers who maintain large herds of $>$ 100 cattle (Fox *et al*., 1993; Baylis & Stevenson, 1998). Such variation in herd size and composition may affect the epidemiology and control of trypanosomiasis in two contrasting ways.

On the one hand, the attraction of savannah species of tsetse (e.g. *Glossina morsitans morsitans* Westwood, *Glossina pallidipes* Austen) to the vicinity of a host is largely a response to host odours: increasing the amount of odour increases the numbers of tsetse attracted to the source, but in a non-linear manner (Hargrove *et al*., 1995). For instance, increasing the dose of host odour over the range of 0.5–60 tonnes of cattle (i.e. one to 120 animals) increased the numbers of *G. m. morsitans* and *G. pallidipes* attracted by, respectively, ~ 1.5- and three-fold for each 10-fold increase in host mass. Hence, in an area where *G. m. morsitans* is the main vector of trypanosomiasis, an individual animal within a herd of 10 or 100 cattle could have a fly load that is 15% (1.5/10) or 2.3% ($1.5^2/100$) that of a solitary animal.

On the other hand, grouping might increase the biting rate on some individuals. For example, animals on the edge of the herd might be exposed to higher probability of attack than those in the middle. Moreover, herds of livestock in traditional African farming systems are heterogeneous, comprising not only a mixture of species (e.g. cattle, sheep, goats and donkeys) within a single herd but also, within each species, animals of different ages and sex. Inter- and intraspecific variation in the olfactory (Vale, 1974a; Torr *et al*., 2006) and visual stimuli (Vale, 1974a; Hargrove, 1976) produced by different hosts as well as their grooming behaviour (Vale, 1977; Torr & Mangwiro, 2000) can lead to variations in the fly load of individual cattle. Consequently, groups of cattle may attract more flies than a solitary animal but, rather than sharing the load equally, some individuals may be attacked more than others. Torr *et al*. (2001) describe just such a phenomenon where an ox penned with a calf bore the brunt of all tsetse feeding, whereas both were bitten when they were penned separately, albeit the ox more than the calf.

These effects may have important practical implications. Firstly, the rate at which an animal is bitten by tsetse is a major factor in the 'risk' of acquiring African trypanosomiasis (Rogers, 1985); the potential differences in rate considered in the examples above might be expected to produce significant differences in risk. Secondly, heterogeneities in the transmission of parasites resulting from variation in biting rates can lead to substantial increases in the basic reproduction number (*R*o) for a disease (Dye & Hasibeder, 1986; Woolhouse *et al*., 1997) and grouping can exacerbate these heterogeneities (Torr *et al*. 2001). Finally, knowledge of how herding practices affect biting rates could improve the cost-effectiveness of disease control by, for example, treating with insecticide or trypanocide those animals that are more likely to be bitten (Eisler *et al*., 2003; Welburn *et al*., 2006).

We report here the results of experiments that evaluated the effects of herd size and composition on the individual-specific risk of cattle being attacked by tsetse. Two experimental approaches were used. In one series of experiments, we quantified the numbers of tsetse attracted to and feeding on groups of cattle of various size and composition. In a second series, we used DNA markers (Torr *et al*., 2001) to identify which individual cattle were bitten within herds of various size, age structure and spatial configuration.

Materials and methods

Studies were conducted between 1999 and 2001 at Rekomitjie Research Station in the Mana Pools National Park of Zimbabwe where *G. pallidipes* and *G. m. morsitans* occur. Studies conducted during the dry season (May–November) were carried out in riverine woodland dominated by *Cordyla africana*, *Lonchocarpus capassa* (both Leguminosae) and *Kigelia pinnata* (Bignoniacaea). In the wet season (December–April), experiments were conducted in deciduous woodland consisting predominantly of *Colophospermum mopane* (Fabaceae).

The study consisted of a series of experiments in which we compared the numbers of tsetse attracted to and feeding on groups of two to 12 cattle. Most experiments included a standard treatment of a single ox which allowed us to compare biting rates on various herds against that on a solitary host.

Effect of herd size and composition on biting rates

We compared the numbers of tsetse attracted to and feeding on groups of four (experiment 1), eight (experiment 2), seven (experiment 3) or 12 (experiment 4) cattle. The herds consisted of adults only, calves only or mixtures of the two and hence we were able to analyse how group size and composition affected the numbers of tsetse attracted and feeding on the herd. The results from these experiments did not, however, provide information on which individual hosts within a herd were bitten.

Heterogeneity of biting within a herd

In a second series of experiments we carried out similar experiments using groups of four (experiment 5), eight (experiment 6) or seven (experiment 7) cattle except that blood-fed tsetse were collected for identification of individual-specific hosts.

'*Traditional*' *herd structure*

Finally, we carried out experiments to analyse the feeding patterns of tsetse attracted to herds which were similar in size and composition to those found in the communal farming areas of Zimbabwe (experiment 8) and assessed whether the treatment of cattle with pyrethroids might affect feeding patterns (experiment 9).

Cattle

Mashona cattle were used in all studies. Adult cattle were treated at 3-month intervals with isometamidium (1 mg/kg; Trypamidium®; Rhône Mérieux, Lyon, France) to prevent trypanosomiasis; any animals that did develop trypanosomiasis were treated with diminazene aceturate (3.5 mg/kg; Berenil®; Hoechst, Frankfurt, Germany). Unless specified otherwise, the cattle were not treated with insecticide. For further details of husbandry practices at Rekomitjie, see Torr & Mangwiro (2000).

Feeding behaviour of tsetse

The numbers of tsetse attracted to and feeding on various herds of cattle were evaluated by placing animals at the centre of an incomplete ring (16 m diameter) of 12 electric nets (Vale, 1974b) following the method of Vale (1977). Cattle were retained in square pens, the sizes of which varied between 4 m^2 and 16 m^2 in order to accommodate one to 12 animals. This prevented them from touching the electric nets but did not restrict their defensive behaviour or the flight of tsetse. For groups of eight to 12 cattle, the pen was fitted with internal partitions to help maintain an even distribution of animals. Experiments were performed during the 2 h preceding sunset, when tsetse are most active (Hargrove & Brady, 1992).

A proportion of the flies approaching or departing from the cattle collided with the electric nets (1.5 × 1.5 m) and fell onto trays where they were retained. If samples were required for DNA analyses, plastic trays were used and flies were collected at 30-min intervals; otherwise corrugated sheets coated with polybutene were used and the flies were collected at the end of each day's experiment. Collected tsetse were sorted by species and sex and according to whether fresh blood was visible through the abdominal wall. The side of the net where each fly was caught was recorded; those caught on the outside or inside of the ring were presumed to be approaching or flying away from the cattle, respectively. Feeding probability (F) was defined as the number of fed flies caught on the inside of the ring expressed as a proportion of the total catch from the inside of the ring (Vale, 1977). The total (i.e. inside + outside) catch of the ring was used as an index of the numbers of tsetse attracted (G). The total catch of *Stomoxys* was also recorded as their abundance affects the feeding behaviour of tsetse (Torr & Mangwiro, 2000; Schofield & Torr, 2002).

The numbers of tsetse attracted to and feeding on various herds of cattle were compared using randomized block designs. Groups of adjacent days were regarded as blocks and treatments were allocated randomly to days within these. Experiments were analysed using GLIM4 (Francis *et al*., 1993). To analyse the numbers of tsetse attracted to a herd, daily catches (n) were transformed to $\log_{10}(n + 1)$ and then subjected to analysis of variance. For convenience, the detransformed mean catches, accompanied by their respective transformed mean ± standard error (SE), are reported. The proportions of tsetse feeding were assessed using a binomial model with a logit link; the significance of changes in deviance was scored by χ^2 or an F-test if the data were overdispersed and required re-scaling (Crawley, 1993).

Fly burden

To provide an index of the mean number of tsetse feeding per host (henceforth termed 'fly burden') for each herd, the product of the total mean daily catch of tsetse (G) and the proportion of tsetse that fed (F) was divided by the number of hosts (adults + calves, $A + C$) in the herd.

Host behaviour

In one experiment only, the defensive behaviour of individual adult and juvenile cattle within a herd was recorded. Previous studies (Baylis, 1996; Torr & Mangwiro, 2000; Schofield & Torr, 2002) have shown that frequency of leg movements is an important determinant of feeding success for tsetse and hence the number of stamps/kicks made by each animal was counted for a 10-min period between 17.00 hours and 18.00 hours. To avoid problems associated with the effect of human odour affecting the behaviour of tsetse (Vale, 1974b), cattle were observed from a position 20 m crosswind from the herd. Observations were repeated for 8 days per animal.

Insecticide-treated cattle

Studies were undertaken to assess whether the selective treatment of cattle with deltamethrin inhibited feeding on a treated animal and/or increased feeding on an adjacent untreated animal. Pairs of adult cattle were placed in adjacent pens within the ring of electric nets for eight afternoons. For the first 4 days of the experiment, neither animal was treated with insecticide but on the morning of the fifth day, one animal was treated with 1% w/v deltamethrin pour-on (Spot-On®; Ecomark, Harare, Zimbabwe) applied along the animal's backline at a rate of 0.1 mL/kg. The relative positions of the animals within the ring were swapped for each pair of days. On each day of the experiment, the total number of tsetse attracted to and feeding on the pair of cattle was recorded and a subsample of fed tsetse were collected for DNA analysis. The experiment was repeated for three pairs of cattle.

Field processing of tsetse for DNA analyses

Tsetse collected from the trays were placed individually into plastic tubes and stored overnight at 4°C. The following morning, the abdomens of the flies were crushed onto filter papers. All materials were handled with disposable gloves and instruments to avoid cross-contamination. The papers were air dried before being sealed in aluminium envelopes and then stored at −10°C. To match bloodmeals with cattle, samples of blood from all cattle at Rekomitjie were also collected onto filter papers. These were dried and stored in the same manner as the bloodmeals.

DNA extraction and microsatellite analysis

DNA was extracted from the filter papers using the protocols of Guglich *et al*. (1994) or Ansell *et al*. (2000) and then amplified with up to five ungulate-specific primer sets (BM4513 and BM1225, Bishop *et al*., 1994; MAP2C, Moore *et al*., 1994; IGF-1, Kirkpatrick, 1992; OLADRB, Paterson *et al*., 1998) following the methods of Torr *et al*. (2001) and Prior & Torr (2002). For each sample, genotypes were determined and the individual-specific source(s) of each bloodmeal was identified by matching meals with cattle genotypes. Multiple meals were identified by the presence of more than two alleles per locus.

Results

Catch composition

A total of 25 705 tsetse were caught, of which 4% were male and 9% female *G. m. morsitans* and 28.8% were male and 58.1% female *G. pallidipes*. For individual experiments, the proportion of *G. pallidipes* varied between 66.2% and 98.0%, with the higher percentages occurring during the dry season (June–November). Pooled results for all species and sexes are presented. *Stomoxys* collected from polybutene-coated trays could not be readily identified as they were coated in polybutene but identification of subsamples collected from the plastic trays showed that the catch ($n = 509$) comprised 70% *Stomoxys niger niger* Macquart, 0.6% *Stomoxys calcitrans* Linnaeus and 31.4% *Stomoxys sitiens* Rhodani.

Herd size and attraction

For each experiment (Table 1), increasing the aggregate mass of the herd increased the mean number of tsetse and *Stomoxys* caught. For instance, increasing the number of hosts from a single adult (herds a, g, m) to groups of four (herd b), eight (herd h) or 12 (herd n) adults increased the catch by factors of 2.2 (203 vs. 92 tsetse/day), 3.0 (172 vs. 58 tsetse/day) and 3.5 (187 vs. 54 tsetse/day), respectively. Conversely, the catch with a group of

Table 1. The detransformed mean daily catch (transformed mean in brackets) of *Glossina* (*G*) and *Stomoxys* from an incomplete ring of electric nets surrounding solitary oxen or herds of cattle comprising various numbers of adults (*A*) and calves (*C*) and the proportion (± standard error [SE]) of fed tsetse (*F*) captured on the inside of the ring of nets. An index of the *per capita* burden of tsetse was calculated as the number of tsetse feeding (*G.F*) divided by the number of cattle ($A + C$).

	Cattle			Catch			Tsetse/host
Herd	Adults (*A*)	Calves (*C*)	Mass (kg)	*Glossina* (*G*)	*Stomoxys*	Fed (*F*)	$(G.F)/(A + C)$
Experiment 1: Ox vs. *four-animal herds (eight replicates: 6 July 1998 to 20 September 1998)*							
a	1	0	400	91.9 (1.968)	62.8 (1.805)	0.569 ± 0.044	52
b	4	0	1600	203.1 (2.310)	117.7 (2.075)	0.506 ± 0.028	26
c	3	1	1300	163.1 (2.215)	78.7 (1.901)	0.573 ± 0.032	23
d	2	2	1000	199.0 (2.301)	84.6 (1.933)	0.515 ± 0.032	26
e	1	3	700	148.4 (2.174)	86.5 (1.942)	0.422 ± 0.035	16
f	0	4	400	95.3 (1.984)	69.7 (1.849)	0.037 ± 0.023	1
		Pooled SE		0.075	0.084		
Experiment 2: Ox vs. eight-animal herds (eight replicates; 21 September 1998 to 6 November 1998)							
g	1	0	400	58.0 (1.771)	3.9 (0.694)	0.636 ± 0.027	37
h	8	0	3200	172.0 (2.238)	7.5 (0.929)	0.644 ± 0.017	14
i	1	7	1100	166.5 (2.224)	9.2 (1.008)	0.413 ± 0.018	9
j	0	7	700	92.2 (1.969)	5.9 (0.838)	0.262 ± 0.026	3
		Pooled SE		0.078	0.123		
*Experiment 3: Ox vs. seven-animal herds (six-replicates; 15 May 2001 to 13 June 2001)**							
k	1	0	400	43.2 (1.645)	46.9 (1.680)	0.718 ± 0.035	31
l	1	6	1000	111.3 (2.050)	94.5 (1.980)	0.669 ± 0.022	11
		Pooled SE		0.102	0.071		
Experiment 4: Ox vs. 12-animal herds (18 replicates; 1 October 1999 to 6 November 1999 and 11–22 March 2000)							
m	1	0	400	53.7 (1.738)	453.6 (2.658)	0.544 ± 0.021	29
n	12	0	4800	187.0 (2.274)	1068.5 (3.029)	0.711 ± 0.010	11
		Pooled SE		0.030	0.040		

*Herd l comprised an ox surrounded by six calves.

four calves (herd f; 95 tsetse/day) with an aggregate mass (400 kg) similar to that of a single adult (herd a, 92 tsetse/day) attracted a similar number of tsetse.

To analyse the general relationship between catch and herd mass, the detransformed mean catches of tsetse and *Stomoxys* for each herd were expressed as a proportion of the catches with a single ox and these proportions were related to the aggregate mass of each herd using a weighted regression, with the weights equal to the reciprocal of the catch variances. The minimally adequate model was obtained using $\log_{10}$(weight) ($F_{1,17} = 27.5$, $P < 0.001$) and species ($F_{1,17} = 5.3$, $P < 0.05$) as predictive parameters (Fig. 1). The results show that increasing herd size increased the absolute number of tsetse and *Stomoxys* attracted to the herd, but the logarithmic relationships between herd size and the numbers attracted leads to a reduction in the mean number of flies per animal.

Feeding success

For groups comprising adult cattle only, herd size had no significant effect on feeding probability (Table 1) except for the 12-animal herd (Table 1, herd n) where the feeding probability was 0.71 compared to 0.54 with a single ox (herd m). This experiment (Table 1, experiment 4) was undertaken during the wet season when the numbers of *Stomoxys* were relatively high. Plotting daily feeding probability of tsetse against the catch of *Stomoxys* (Fig. 2a) shows that the range of feeding probabilities for individual cattle was more variable than that for the herd, with the lower probabilities occurring on days when *Stomoxys* were particularly abundant. Other studies have shown that the feeding success of tsetse is inversely correlated with rates of defensive leg movements which, in turn, are positively correlated with the numbers of *Stomoxys* feeding on the host (Torr & Mangwiro, 2000). Thus, increasing herd size might decrease the per capita number of *Stomoxys* and hence increase the feeding rate of tsetse. In support of this, there was a significant ($F_{1,32} = 50.4$, $P < 0.001$) effect of the per capita catch of *Stomoxys*, estimated by dividing the daily catch by the herd size, on feeding probability (Fig. 2b); the minimally adequate model of feeding probability included per capita catch of *Stomoxys* but not herd size, suggesting that the higher feeding probability with the 12-animal herd resulted from a reduction in *Stomoxys*-related defensive behaviour.

Tsetse attracted to herds comprised entirely of young cattle had low feeding probabilities (Table 1, herds f and j). However,

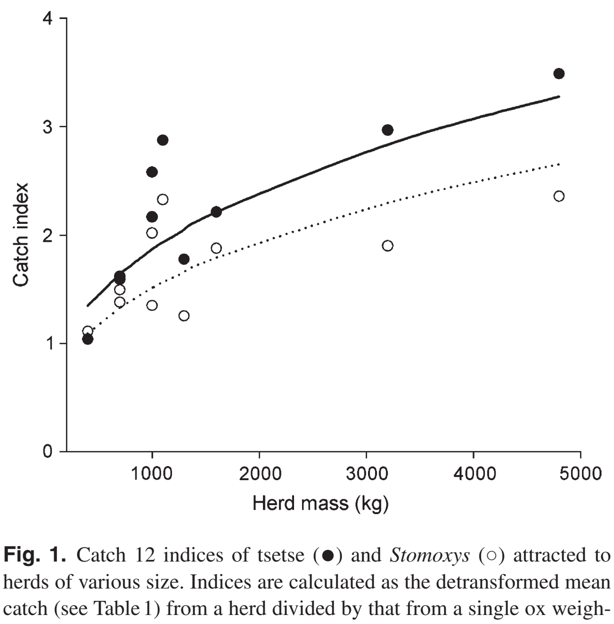

Fig. 1. Catch 12 indices of tsetse (●) and *Stomoxys* (○) attracted to herds of various size. Indices are calculated as the detransformed mean catch (see Table 1) from a herd divided by that from a single ox weighing 400 kg. Lines fitted by regression of $\log_{10}$ (herd mass) against $\log_{10}$ (catch index); regression co-efficients for tsetse and *Stomoxys* were 0.41 (± 0.070, standard error) and 0.25 (± 0.093), respectively.

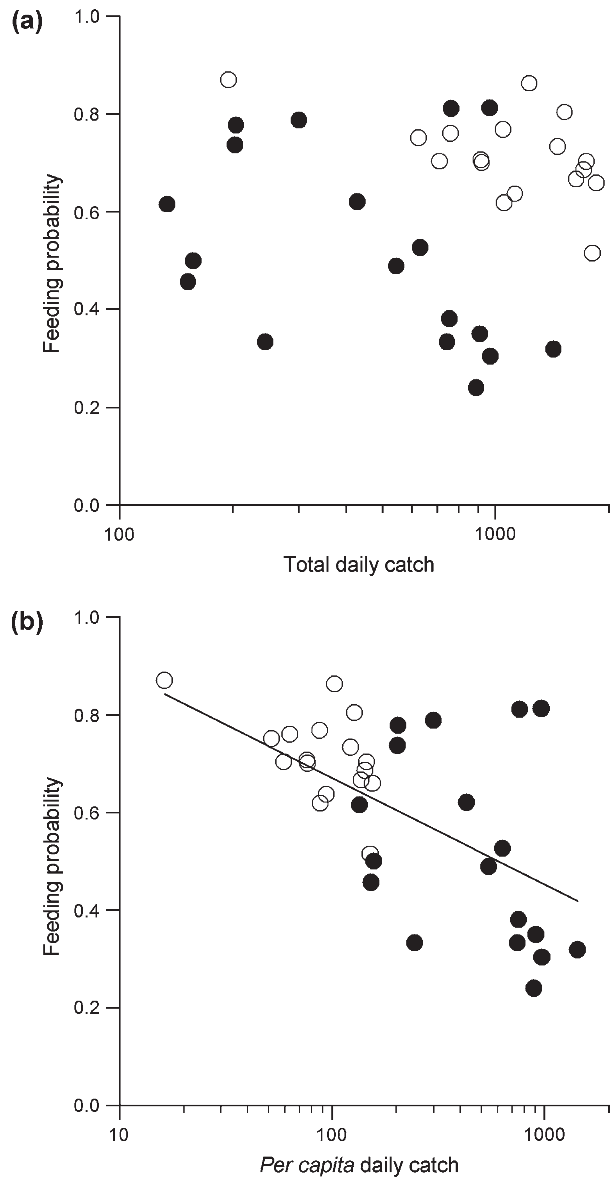

Fig. 2. Feeding probability of *Glossina* plotted against (a) total daily catch of *Stomoxys* or (b) per capita catch of *Stomoxys* for a single ox (●) or a herd of 12 cattle (○). Line fitted by logistic regression.

the probabilities for tsetse attacking mixed herds were not significantly different from all-adult ones. For instance, tsetse attracted to four-animal groups containing one to three calves (Table 1, herds c–e) had a feeding probability of 0.42–0.57 compared with 0.03 if all the animals were calves (Table 1, herd f). The higher feeding rate on mixed herds suggests that tsetse fed selectively from the adults within the herd.

Fly burden

In general, fly burden (i.e. fed tsetse/host) declined with increases in (a) herd size and (b) the proportion of juvenile hosts within the herd (Table 1). For instance, in experiment 1 (Table 1), an individual adult (herd a) had a fly burden of 52 tsetse/day, compared with 26 tsetse/day for a group of four adults (herd b) and just one tsetse/day for a group of four calves (herd f). Similar trends were apparent in experiments 2–4 (Table 1).

Individual-specific feeding patterns: four-animal groups

Comparisons between (a) a single ox, (b) four oxen, (c) four calves and (d) an ox and three calves (Table 2, experiment 5) confirmed the earlier findings (Table 1, experiment 1) that groups that included at least one adult had significantly higher feeding rates than calf-only groups.

Most tsetse (21/22, 95%) attracted to a single ox were found to have fed on that animal; the remaining (1/22, 5%) fly was found to have blood from another ox that had been in the ring on a previous day. The low feeding rate on the all-calf group meant that only four fed tsetse were available for analysis. All of these contained blood from an ox that had been in the ring on a previous day rather than from the calves. This result suggests that the actual feeding rate on calves may be lower than that suggested by the ring of nets (Table 1, experiment 1; Table 2, experiment 5) where fed flies were assumed to have fed on the cattle within the ring. For groups comprising a single ox and three calves, 98% ($n = 39$) of meals were from the adult; one meal (2%) was from an ox that had been in the ring on a previous day and no meals were from the calves. The results for groups of four adults showed that some hosts were particularly favoured. Oxen #537 (mass = 470 kg) and #219 (370 kg) were present in each of the three herds tested. Meals taken from #537 accounted for 55% ($n = 24$), 41% ($n = 18$) and 62% ($n = 48$) of all meals, whereas those taken at equivalent times from #219 accounted for 13%, 24% and 12% of all meals, respectively. A total of 9% (8/88) of meals taken from the adult groups comprised blood from two of the cattle within the ring but no mixed meals were found with the other groups.

Eight-animal groups

Analysis of the feeding patterns of tsetse attracted to groups of seven calves and one ox (Table 2, experiment 6) showed that

Table 2. Detransformed mean catches (transformed means in brackets) of *Glossina* and *Stomoxys* and proportion (± standard error [SE]) of *Glossina* fed from experiments where DNA markers were used to assess individual specific feeding patterns.

Herd	Cattle		Mass (kg)	Catch		Fed ± SE
	Adults	Calves		*Glossina*	*Stomoxys*	
Experiment 5: four-animal herds (four replicates; 11–26 September 1999)						
o	1	0	400	29.8 (1.489)	636.1 (2.804)	0.351 ± 0.056
p	4	0	1600	73.3 (1.871)	924.8 (2.967)	0.489 ± 0.037
q	0	4	400	42.2 (1.635)	1889.7 (3.277)	0.061 ± 0.032
r	1	3	700	48.9 (1.698)	1284.8 (3.109)	0.409 ± 0.048
		Pooled SE		0.090	0.092	
Experiment 6: eight-animal herds (four replicates; 27–30 September 1999)						
s	1	7	1100	78.1 (1.898)	774.5 (2.890)	0.401 ± 0.036
				0.053	0.278	
Experiment 7: seven-animal herds (six-replicates; 8 April 2001 to 16 May 2001)						
t	6	0	2400	182.7 (2.264)	150.7 (2.181)	0.544 ± 0.017
u	0	6	600	115.9 (2.068)	133.0 (2.127)	0.262 ± 0.023
v	7	0	2800	152.8 (2.187)	126.1 (2.104)	0.733 ± 0.017
w*	1	6	1000	124.0 (2.097)	113.0 (2.057)	0.658 ± 0.021
		Pooled SE		0.063	0.071	
Experiment 8: eight-animal herds (12 replicates; 7–12 April 2000 and 8–13 October 2000)						
x	6	2	1960	171.0 (2.236)	97.7 (1.994)	0.742 ± 0.012
				0.028	0.107	
Experiment 9: two-animal herds (12 replicates; 10–20 October 2001 and 5–22 February 2002)						
y	2	0	800	80.7 (1.912)	193.1 (2.288)	0.651 ± 0.023
z†	2	0	800	56.8 (1.762)	157.6 (2.200)	0.596 ± 0.025
		Pooled SE		0.078	0.088	

*Herds comprised an ox surrounded by six calves or six adults.
†Herds comprised one insecticide-treated animal and one untreated animal.

92% ($n = 63$) of identified meals were from the single ox, 3% (2/63) from the calves and 5% (3/63) from other oxen at Rekomitjie that were not in the ring on the day of the experiment. Thus, even when the smaller hosts were more numerous, tsetse were biased towards feeding from older cattle. No mixed meals were detected in the samples from these eight animal herds.

Spatial effects

To assess whether the spatial arrangement of hosts affected host selection, we analysed bloodmeals from tsetse attracted to a group of (a) six calves or (b) six adults, with or without an adult in the centre of the group. Animal #537 was selected as the central animal as it was known to be preferred to other adult cattle (above; see also Torr *et al*. 2001).

There were no significant differences between the numbers of tsetse or *Stomoxys* attracted to the different groups, but there were clear and significant differences in the feeding probabilities (Table 2, experiment 7). As expected, the calf-only herd (herd u) had a significantly lower feeding probability (0.26) than the other groups (0.54–0.73). Placing ox #537 at the centre of the group of calves (herd w) increased the feeding probability from 0.26 to 0.66, with 89% of the meals coming from ox #537 (Table 3, herd w). Placing the same ox in the middle of a group of six adults also increased the feeding probability from 0.54 to 0.73, with 49% (Table 3, herd u) of bloodmeals coming from ox #537. The feeding probabilities for ox #537 alone (0.72; Table 1, experiment 3, herd k) or surrounded by calves (0.66; Table 3, herd w) or adults (0.73; Table 3, herd u) were remarkably similar.

Host behaviour

Previous studies have suggested that the high feeding probability on ox #537 is the result of its low rate of defensive behaviour (Torr & Mangwiro, 2000) and observations of the frequency of defensive foot movements confirmed this: ox #537 averaged 8.3 (range 3–16) stamps per 10-min observation period compared with mean stamping rates of 11.6–26.0 for the other adults and 27.2–55.7 for the calves.

Balanced herds

In the farming systems typical of southern Africa, cattle herds generally consist of a mixture of oxen, cows, heifers and calves. Studies were therefore made of the feeding patterns of tsetse attracted to herds comprising two oxen, four heifers/cows and two calves, this being the typical size and composition of herds owned by households in the tsetse-infested areas of northern Zimbabwe (Hargrove *et al*., 2003). The study was performed in April and October 2000 and in each of these months, two herds were composed from a pool of 16 different individual cattle. A lion attack during the April experiment resulted in the loss of one test animal, which was replaced by another of similar age, size and sex.

The eight animals comprising each herd were ranked according to weight. As expected, the number of meals per ranked animal show that larger cattle tended to be bitten more than smaller ones (Fig. 3); 45% (207/460) of meals were derived from the heaviest animal within a herd compared with just 1% (3/460) from the smallest. For particular groups, however, the proportion of meals from the heaviest animal varied between 23.1% (30/130) and 77.0% (104/135), and the heaviest animal was not always the most fed upon for a particular herd. Individual specific differences in host behaviour contributed to this variation, as illustrated by the two herds that contained animal #537, an ox known to display low rates of host defensive behaviour (see above). In one case, in which this animal was the heaviest in the herd, it provided 77.0% (104/135) of the meals. In another case, when it was the second heaviest, it gave 59.8% (55/112) of the meals compared with 27.2% (25/112) from the heaviest animal. About 9% (40/460) of tsetse contained blood from two herd members, and 40% (16/40) of these mixed meals comprised blood from the two heaviest cattle in a herd.

Insecticide-treated cattle

Treating one of the pair of animals with deltamethrin had no significant effect on the mean catch of tsetse or the feeding probability (Table 2, experiment 9). The proportion of meals from each individual was also not affected significantly by treating one of the animals with deltamethrin. Prior to treatment, the

Table 3. Feeding patterns of tsetse attracted to a group of six adult cattle or calves with or without an 'attractive' host (ox #537, bold values) placed at the centre of the groups. Data show the percentage of *n* flies containing blood from each animal, denoted by its tag number and weight. Percentages sum to > 100 because a proportion of tsetse had taken mixed meals (*m*) with blood from two of the hosts. For other details of the mean daily catch and overall feeding rate, see Table 2, experiment 7.

			Herd members													
Herd ref.	*n*		Adults							Calves						*m* (%)
		Tag nos.	#214	#219	#572	#594	#597	#274	**#537**	#C573	#C214	#C012	#C588	#C591	#C238	
		Weight (kg)	395	395	290	465	350	270	**400**	115	55	85	80	80	80	
t	79		17.7	12.7	15.2	24.1	1.3	31.6	—	—	—	—	—	—	—	2.5
u	80		7.5	17.5	10.0	12.5	5.0	3.8	**48.8**	—	—	—	—	—	—	5.0
v	21		—	—	—	—	—	—		57.1	9.5	4.8	9.5	14.3	9.5	4.8
w	92		—	—	—	—	—	—	**89.1**	5.4	0.0	4.3	0.0	1.1	2.2	2.2

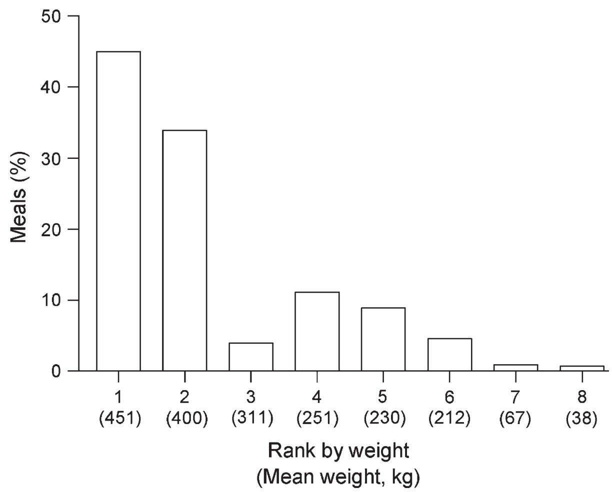

Fig. 3. Proportion of meals taken from cattle ranked by their weight. Data derived from pooled analyses of the feeding patterns of tsetse ($n = 460$) attracted to five different herds of eight cattle studied in April and October 2000. Mean weight of each rank is shown in brackets. See Table 2, experiment 8 for general catch and feeding rate statistics.

proportions of meals from the three test animals were, respectively, 0.86 ($\pm$ 0.03, $n = 112$), 0.51 ($\pm$ 0.06, $n = 69$) and 0.56 ($\pm$ 0.09, $n = 36$) compared with 0.78 ($\pm$ 0.07, $n = 94$), 0.38 ($\pm$ 0.11, $n = 34$) and 0.72 ($\pm$ 0.14, $n = 18$) after they had been treated.

Discussion

The present results confirm that herding in cattle reduces mean per capita fly burden, but also show that there is substantial individual-specific variability within herds.

Herd size

The present indications for the effect of herd size are broadly in line with those of Hargrove *et al*. (1995), who showed that 10-fold increases in herd mass increased the catch of *G. pallidipes* 2.1–2.8 times. However, Hargrove *et al*. (1995) reported a 4.6-fold increase in *Stomoxys* catch for each 10-fold increase in dose, whereas our results indicate that the catch increases for *Stomoxys* were consistently less than those for tsetse. This discrepancy may reflect differences in the species compositions of *Stomoxys* populations involved; Holloway & Phelps (1991) caught *Stomoxys* at Rekomitjie at the same time that Hargrove *et al*. (1995) performed their studies (January–May 1988) and found that *S. calcitrans* predominated, whereas we caught few *S. calcitrans* but many *S. n. niger* and *S. sitiens*.

Nonetheless, past and present results suggest that for all these species of biting fly, the mean number of flies/host is reduced with increases in herd size. Assuming that the biting rate for tsetse is 2.5-fold lower for a 10-fold increase in herd size, then herds of 10 and 100 animals will have biting rates that are 25% and 6% of the rate for a solitary animal. Herds of these sizes are typical of those owned by peasant farmers in northern Zimbabwe (13 cattle/herd) and commercial ranches in Tanzania (150 cattle/herd) (Hargrove *et al*., 2003).

Is there any empirical evidence that herding has reduced the incidence of trypanosomiasis? Laboratory studies of the transmission of *Trypanosoma congolense* and *Trypanosoma vivax* by tsetse suggest transmission efficiencies of 20–46% (Harley & Wilson, 1968; Wilson *et al*., 1972; Otieno & Darji, 1979). By contrast, Baylis (1997) compared the biting rate on a single ox and disease incidence in a herd of 40 cattle and found that the incidence was just 0.8% and 2.4% of the estimated daily number of bites from tsetse infected with *T. congolense* or *T. vivax*; even allowing for possible errors in the numbers of tsetse attracted to a host and variation in the density of tsetse only increased the efficiency estimates to 2.5% (*T. congolense*) and 5.3% (*T. vivax*). Baylis (1997) argued that the discrepancies between field and laboratory estimates were the result of flaws in the laboratory studies. An alternative explanation, suggested but not explored by Baylis, is that being in a herd caused a lower-than-expected incidence of trypanosomiasis. The transmission efficiencies reported by Baylis (1997) suggest that there were 119 *T. congolense*- and 41.7 *T. vivax*-infected bites on each herd member. Using a value of 0.4 for a power of bait mass (i.e. a 2.5-fold increase in catch for each 10-fold increase in herd size) indicates that a herd of 40 cattle would receive 4.37 times ($40^{0.4}$) more infective bites than a solitary animal. This implies that the herd received 520 (4.37×119) *T. congolense*- and 182 (4.37×41.7) *T. vivax*-infective bites per case, with per capita biting rates of 13 (520/40) and 4.6 (182/40) and transmission efficiencies of 8% and 22%, respectively. If we use the adjusted estimates provided by Baylis (1997) (i.e. 2.5–5.3%), then herd-adjusted efficiencies are 23% and 48%, respectively. These values are remarkably similar to the laboratory estimates, given the various approximations involved, and suggest that the low incidence of disease observed by Baylis (1997) was the result of, at least partially, the protective effects of being in a herd.

Host heterogeneity

The present study not only confirms previous studies (Torr & Mangwiro, 2000; Torr *et al*., 2001, 2006) showing that older cattle are bitten more often than younger ones, but also shows that this bias occurs even when the older host is at the centre of a group and hence outnumbered and screened by younger cattle. The bias towards particular cattle within a herd means that herding can increase the biting rate for some hosts and reduce it for others. For instance, surrounding a single ox with six calves increased the total number of tsetse attracted. If it is assumed that all animals were bitten equally the mean biting index declined from 31 to 11 (Table 1, experiment 3). However, analysis of the individual cattle bitten showed that 89.1% of meals were from the single ox (Table 3, herd w) and thus the presence of the calves doubled the biting rate on the ox, from 31 to 66 ($111.3 \times 0.669 \times 0.891$). By contrast, placing a single placid ox within a group of six less placid cattle decreased the mean biting rate on the six from 16 to 10. In summary, adding cattle increases the numbers of tsetse attracted to a herd but the composition of the herd determines which animals carry this extra burden.

Herd size and entomological inoculation rates

The probability of a tsetse bite resulting in disease is the product of the prevalence in the vector population (p) and the probability that a bite from an infected fly results in an infection (b_1). Taking values of 0.05 and 0.29 for p and b_1 as representing *T. vivax* (Rogers, 1988), then the overall probability of being infected per bite is 0.0145 and, conversely, $1 - 0.0145 = 0.9855$ of not being infected. If a host is bitten by n flies, then the probability of not being infected is 0.9855^n and hence the probability of infection is $1 - 0.9855^n$. For a homogeneous herd of hosts, in which the numbers of tsetse attracted to a herd is a power (0.4) of the number of animals in the herd (c), the number of tsetse biting each animal relative to that biting a solitary animal is $c^{0.4}/c$. The consequence of these relationships is that if the biting rate is < 100 bites/solitary animal/day, then grouping cattle into herds of ~ 50 animals reduces the infection risk by 90% (Fig. 4). At higher biting rates (e.g. > 1000 bites/solitary animal/day), herding provides much less, if any, benefit. At Mkwaja ranch in Tanzania (Hargrove *et al*., 2003), cattle were grouped into herds of 150 cattle; the present results suggest that this practice would have had a significant impact on disease incidence.

The relationship is slightly different for heterogeneous herds. Considering first solitary animals, let us assume that oxen, cows and calves weigh 450 kg, 250 kg and 50 kg, respectively. Using a power of 0.4 for the relationship between mass and the numbers of tsetse attracted to a host, then a solitary cow or a calf would attract 79% and 42% of the number attracted to an ox. These values are in close accord with empirical comparisons of the numbers of tsetse attracted to oxen, cows and calves (Torr *et al*., 2006). If we further assume that the feeding probability on a solitary ox, cow or calf is 0.6, 0.45 and 0.11, respectively (Torr & Mangwiro, 2000), then the biting rates on a solitary cow or calf will be 75% and 8%, respectively, of that on an ox.

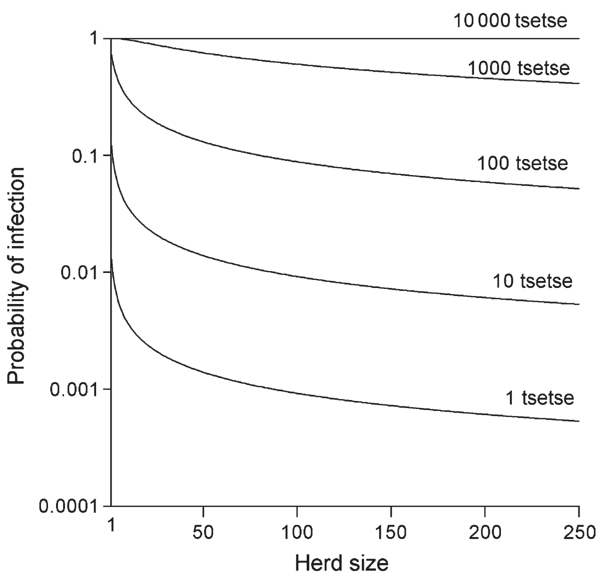

Fig. 4. Daily probability of infection for oxen in homogeneous herds of various size, assuming a single ox is bitten by 1–10 000 tsetse/day. For further details, see text.

To examine what happens with a heterogeneous group of hosts, we assumed that a herd comprised 25% oxen/bulls, 50% cows/heifers and 25% calves (Hargrove *et al*., 2003) with each type weighing 450 kg, 250 kg and 50 kg, respectively. The number of tsetse attracted to a herd was a simple power (0.4) of the herd's mass, as before, and the proportion of meals taken from the oxen, cows and calves in a herd was 78%, 20% and 2%, respectively (Fig. 3). We further assumed that a solitary ox was bitten by 100 tsetse/day and from this we calculated the numbers of tsetse biting each host-type and hence the individual-specific probability of infection. The results (Fig. 5) show three important features. First, as the herd now comprises a number of smaller hosts, the number of tsetse attracted per host is smaller; a herd of 20 heterogeneous cattle weighs 5000 kg and hence attracts 2.6 times as many tsetse as a single 450-kg ox, whereas 20 oxen weigh 9000 kg and attract 3.2 times as many. Thus, the mean per capita fly load for the heterogeneous herd is slightly smaller than that of the homogeneous one. For oxen, there is a slight *increase* in infection probability with a herd of four animals, but thereafter infection risk declines with increasing herd size, although the protective value of a mixed herd is less than that provided by a homogeneous group. For cows and calves, the benefits of herding are greater, with an individual's risk of infection reduced by $> 90\%$ by being in a herd of just 28 cattle; for a calf in such a herd, the daily risk of trypanosomiasis (0.0093) is ~ 1% of that for a solitary ox (0.768). These results may explain, at least in part, the lower incidence of trypanosomiasis in young and female cattle (Trail *et al*., 1994; Van den Bossche *et al*., 2000; Rowlands *et al*., 2001).

The effects of herd size and composition on the feeding behaviour of tsetse are likely to be qualitatively similar with

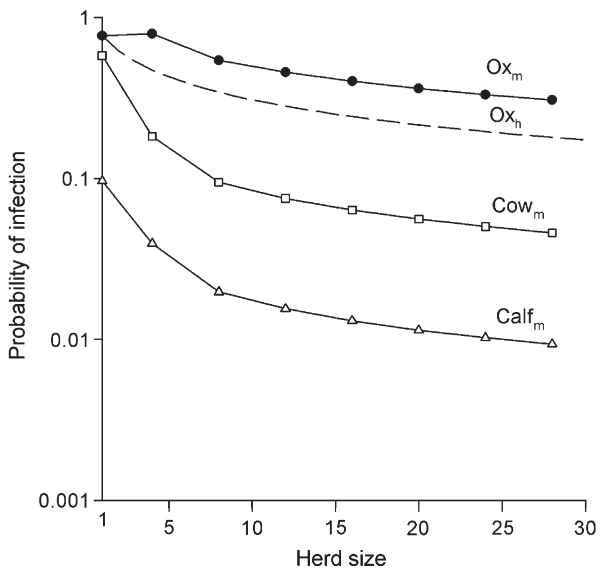

Fig. 5. Daily probability of infection for an ox (●, Ox_m), cow (□, Cow_m) or calf (Δ, $Calf_m$) in mixed (25% oxen, 50% cows, 25% calves) herds of various size. The dotted line shows probability of infection for an ox (Ox_h) in a homogeneous herd of oxen. Infection probability assumes that a solitary ox is bitten by 100 tsetse/day. For further details, see text.

other Dipteran vectors. Most species of biting fly are attracted to their hosts by host odours and the numbers attracted to the host are generally a power function of bait mass (Gibson & Torr, 1999). Moreover, the feeding success of cattle-feeding species of *Stomoxys* (Prior, 2003), *Anopheles* (Prior & Torr, 2002) and Tabanidae (Foil *et al*., 1985) is greater on older/larger animals.

Implications for control of vector-borne diseases

The use of insecticide-treated cattle is an increasingly important means of controlling tsetse, especially for community-based schemes where livestock keepers aim to control tsetse themselves rather than relying on governments or donors. However, the technique is frequently too expensive for poor farmers to sustain and there are concerns that this technique kills non-target organisms and reduces enzootic stability for some tick-borne diseases (Eisler *et al*., 2003).

The current results suggest that treating only the larger/older animals within a herd might address these concerns. For heterogeneous herds of cattle (e.g. Fig. 3), treating half the herd, applying insecticide to only the larger individuals, would be slightly less effective than treating the entire herd but would reduce the amount of insecticide used. Such a strategy might be undermined by the excito-repellent effects of pyrethroids for at least some vectors (Curtis *et al*., 1996). However, the present results suggest that tsetse were not repelled from deltamethrin-treated animals, and previous studies of individual animals also suggest that treating livestock with deltamethrin does not affect the behaviour of tsetse feeding on cattle (Baylis *et al*., 1994; Vale *et al*., 1999; Torr *et al*., 2007).

Perhaps more importantly, not treating young cattle with insecticide increases the probability that they will be bitten by ticks and so develop immunity to tick-borne diseases. Hence, the risk of disrupting enzootic stability for these tick-borne diseases would also be reduced. Combining this selective treatment of hosts with the restricted application of insecticide to those body regions where most tsetse feed (Torr *et al*., 2007) would reduce insecticide costs by 90%, compared with the current regime of treating the entire herd, and the impact on non-target organisms.

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