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Less is more: restricted application of insecticide to cattle to improve the cost and efficacy of tsetse control

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Abstract. Studies were carried out in Zimbabwe of the responses of tsetse to cattle treated with deltamethrin applied to the parts of the body where most tsetse were shown to land. Large proportions of *Glossina pallidipes* Austen (Diptera: Glossinidae) landed on the belly (~ 25%) and legs (~ 70%), particularly the front legs (~ 50%). Substantial proportions of *Glossina morsitans morsitans* Westwood landed on the legs (~ 50%) and belly (25%), with the remainder landing on the torso, particularly the flanks (~ 15%). Studies were made of the knockdown rate of wild, female *G. pallidipes* exposed to cattle treated with a 1% pour-on or 0.005% suspension concentrate of deltamethrin applied to the (a) whole body, (b) belly and legs, (c) legs, (d) front legs, (e) middle and lower front legs, or (f) lower front legs. The restricted treatments used 20%, 10%, 5%, 2% or 1% of the active ingredient applied in the whole-body treatments. There was a marked seasonal effect on the performance of all treatments. With the whole-body treatment, the persistence period (knockdown > 50%) ranged from ~ 10 days during the hot, wet season (mean daily temperature > 30 °C) to ~ 20 days during the cool, dry season (< 22 °C). Restricting the application of insecticide reduced the seasonal persistence periods to ~ 10–15 days if only the legs and belly were treated, ~ 5–15 days if only the legs were treated and < 5 days for the more restricted treatments. The restricted application did not affect the landing distribution of tsetse or the duration of landing bouts (mean = 30 s). The results suggest that more cost-effective control of tsetse could be achieved by applying insecticide to the belly and legs of cattle at 2-week intervals, rather than using the current practice of treating the whole body of each animal at monthly intervals. This would cut the cost of insecticide by 40%, improve efficacy by 27% and reduce the threats to non-target organisms and the enzootic stability of tick-borne diseases.

Key words. *Glossina*, cattle, deltamethrin, insecticide-treated cattle, trypanosomiasis, tsetse, vector control, Zimbabwe.

Introduction

Treating cattle with insecticide is an increasingly important means of controlling tsetse flies as livestock keepers, rather than government or donor agencies, are now largely responsible for funding and implementing interventions against trypanosomiasis (Eisler *et al.*, 2003). Consequently, cheap methods of control that can be applied by farmers themselves are more likely to be sustainable than expensive and complex alternatives such as aerial spraying or the sterile insect technique. Moreover, farmers will tend to select interventions that control several diseases rather than just one; treating cattle with insecticide to control tsetse may also control tick-borne diseases, whereas deploying insecticide-treated targets will not (Vale & Torr, 2004). However, although the use of insecticide-treated cattle has several advantages, it also has problems.

To tackle trypanosomiasis, livestock keepers can control tsetse and/or treat their cattle with trypanocides. The high mobility of tsetse means that to control them successfully, tsetse control must be applied over a large area (~ 1000 km^2) for at

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least a year. Smaller operations, conducted over ~ 500 km^2, can reduce the incidence of trypanosomiasis (Hargrove *et al.*, 2000, 2002) but will not eliminate a tsetse population and hence the intervention must be sustained indefinitely. In practice, this means treating cattle with a synthetic pyrethroid at 2–4-week intervals for many months, if not years (Hargrove *et al.*, 2000). By contrast, a single dose of a curative trypanocide, such as diminazene aceturate, can cure an animal of disease for less than the cost of a single monthly dose of pyrethroid using the currently recommended regimen (Shaw, 2004). Moreover, the benefits of using drugs accrue largely to the individual user and their efficacy is not dependent on the participation of other livestock keepers. Hence, many individual livestock owners choose the private, immediate and obvious benefits of using trypanocides rather than the more expensive, public and longterm benefits of controlling tsetse. Ultimately, however, a strategy based on the exclusive use of trypanocides is not sustainable: drug resistance is increasing (Holmes *et al.*, 2004) and livestock systems 'protected' by trypanocides are much less productive than those where tsetse and trypanosomiasis have been eliminated (Barrett, 1997; Shaw, 2004). Nonetheless, the use of trypanocides is widespread, with ~ 35 million doses administered each year (Holmes *et al.*, 2004), whereas the use of insecticide-treated cattle is patchy and seldom sustained.

Moreover, the routine treatment of cattle with insecticides may be undesirable as widespread treatment of cattle with pyrethroids can lead to acaricide resistance in tick populations (Bruce & Wilson, 1998), disruption of enzootic stability for tick-borne diseases (Eisler *et al.*, 2003) and reductions in the invertebrate fauna associated with the breakdown of cattle dung (Vale & Grant, 2002; Vale *et al.*, 2004). Thus, although the use of insecticide-treated cattle does have beneficial elements, there is a need to make this method as cheap and easy to use as trypanocides, while aiming to reduce its impact on non-target organisms.

Experience has shown that, in order to reduce costs, some farmers treat their cattle at 2–4-month intervals rather than at the recommended intervals of ≤ 1 month (S. Torr, unpublished data). Data on the persistence of insecticides applied to cattle are, however, equivocal: results from Zimbabwe, for example, suggest that formulations are effective for 5–50 days (Vale *et al.*, 1999), whereas in Burkina Faso insecticide may be effective for ~ 75 days (Bauer *et al.*, 1992). Clearly, there is an urgent need to establish a sound recommendation for the most cost-effective treatment regime.

Opportunities to reduce cost have been suggested by studies showing that at least two important vectors of trypanosomiasis, *Glossina pallidipes* and *Glossina morsitans morsitans*, feed largely on the belly and lower legs of older and larger cattle (Torr & Hargrove, 1998; Vale *et al.*, 1999; Torr *et al.*, 2001); treating only the feeding sites of tsetse on older and larger cattle could control these vectors at a tenth of the current cost. This selective approach also reduces the risks to dung fauna (Vale & Grant, 2002) and the enzootic stability of tick-borne diseases (Eisler *et al.*, 2003). If insecticide costs could be reduced by 90%, tsetse control might be sustainable as the method would be cheaper to use than trypanocides. This paper reports the results of studies of the mortality and behaviour of *G. pallidipes* and *G. m. morsitans* feeding on cattle treated with insecticides applied to the body regions where most tsetse land.

Materials and methods

General methods

Most of the research was carried out between May 2002 and March 2005 at Rekomitjie Research Station (16°08′ S, 29°24′ E) in the Zambezi Valley of Zimbabwe where *G. pallidipes* is abundant. Limited studies were also undertaken with *G. m. morsitans* near Makuti (16°19′ S, 29°15′ E), some 25 km southwest of Rekomitjie. Mashona cattle (mean weight ≈ 400 kg) were used for all tests at both sites. When not directly used in experiments, the cattle grazed for ~ 8 h/day in the surrounding woodland or were kept in separate pens that were exposed to wind and rain but had a roof of netting which provided 50% shade, typical of the shade in woodland grazing areas. Treated and untreated cattle were penned separately and grazed > 500 m apart to avoid insecticide transfer.

Landing behaviour of tsetse

Two methods were used to observe the landing behaviour of tsetse. In one method, observations of the site and duration of landing on insecticide-treated and untreated cattle were made by two observers hidden in a ventilated pit (Hargrove, 1976) which prevented human odours and visual stimuli affecting the behaviour of tsetse (Vale, 1974). Every 10 min, the number, species and location of the tsetse on an ox were classified into nine regions (Fig. 1). Between each count, the observers recorded the duration that individual tsetse rested on the host. The observations were repeated for four untreated cattle and four cattle treated with a 1% deltamethrin pour-on formulation (Spot-On™, Ecomark, Harare, Zimbabwe) applied at the recommended rate of 1 mL/10 kg along the spine of the cattle. Each

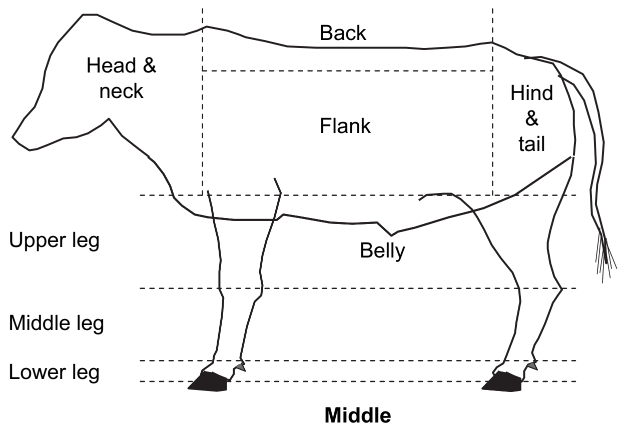

Fig. 1. Regions for classifying location of tsetse. The front and rear legs were each divided into three regions: upper leg (above the hock or knee); middle leg (above the fetlocks), and lower leg (pasterns, below the fetlocks).

animal was observed continuously between 16.00 hours and 18.00 hours for 5 days. Untreated and insecticide-treated cattle were observed on adjacent days, following a randomized block design.

In a second series of studies, observations were made by exposed observers sitting or standing near single oxen. In these studies, the distribution of feeding flies was recorded in addition to the landing distribution.

Insecticides

Cattle were treated separately with one of the following commercial formulations of deltamethrin (Ecomark): (a) Decatix™ 50 g/L suspension concentrate of deltamethrin diluted with water to a concentration of 0.05 g/L and applied with a knapsack sprayer to the entire body of an ox or to selected parts using either a knapsack sprayer or smaller hand sprayer, or (b) Spot-On™ 10 g/L solution of deltamethrin in oil applied to selected parts of the ox's body using a syringe.

Bioassays

Unless stated otherwise, bioassays were performed with wild female *G. pallidipes*. Each trial involved at least four oxen. To provide controls for each trial, one animal was sprayed all over with the standard formulation of Decatix™ and a second animal was left untreated. The remaining two or more animals were treated with insecticides applied to restricted regions of their bodies.

All treatments were applied at about 09.00 hours. Between 15.00 hours and 18.00 hours on the day of treatment and for 10–40 days thereafter, animals were sited ≥ 500 m apart within 1 km of the research station. Engorged tsetse were collected from each of the four cattle using handnets and transferred to glass tubes (2.5 cm wide × 7.5 cm long) sealed by netting at one end and a cork at the other. A clean net was used for each capture attempt in order to minimize contamination. The body region (front leg, hind leg, belly, other) where each fly was collected was recorded. Tubes containing the collected flies were stored in a humidified, polystyrene box. With each ox, catching continued until dusk or until 30 flies had been caught, whichever was sooner. The flies were then transferred to an insectary held at ~ 25 °C and ~ 70% RH for 2 h (i.e. ~ 3.5 h after exposure), at which point the number of flies knocked down was scored. The duration of each trial varied according to the persistence of the standard (whole-body) treatment but usually ceased when the knockdown from the standard whole-body treatment had declined to ~ 10%.

Studies of the landing sites of tsetse (see below) suggested a number of application regimes ranging from treating the belly and legs to more restricted applications of areas such as the front lower legs only (Fig. 1). Decatix™ was sprayed over the entire target region(s), whereas Spot-On™ was applied only to the top on the assumption that it would spread downwards. Hence, if Spot-On™ was applied to the top of a leg, the entire leg was regarded as having been treated. For each regime, test animals were treated with either Spot-On™ or Decatix™ and each treatment was replicated at least twice, covering the hot, wet and cool, dry seasons.

Statistical analyses

All analyses were carried out with GLIM4 (Francis *et al.*, 1993). Data were binomial in nature and were therefore analysed using a binomial model and a log link. To compare differences in the proportions of tsetse landing on specific body regions (e.g. legs), the number of tsetse observed on the body region and the total number of tsetse observed on that day were used as the response variable and the binomial denominator, respectively. For the bioassay data, the number of tsetse knocked down by a particular treatment was used as the response variable and the total number of flies exposed to it was the binomial denominator. To gauge the effective life of a treatment, changes in the knockdown rate over time were assessed by regressing knockdown rate against the natural log of the days. The time taken for knockdown to decline to 50% (KD50) and the 95% confidence interval (95% CI) of the time were estimated using Fieller's theorem (Crawley, 1993). This time is termed the persistence period.

In general, the maximal model was first fitted to the data and the interactions and main effects were then removed stepwise (Crawley, 1993). Changes in deviance were evaluated by chi-square or *F*-test after re-scaling if over-dispersion was evident (Crawley, 1993). The critical level of probability for significance was taken to be $P < 0.05$.

Landing durations on insecticide-treated and untreated cattle were analysed by fitting the times to a Weibull distribution following Crawley (1993). The distribution is determined, in part, by the shape parameter (α) which is 1 if the duration of times is exponentially distributed.

Results

Distribution of tsetse on cattle

In the studies carried out with the observers in the pit, there was no significant difference within species in the distribution of tsetse landing on untreated cattle or those treated with a whole-body application of insecticide and therefore the data were pooled within species. This gave two datasets, which, taken with the results produced without the observation pit (i.e. with exposed observers), gave a total of five datasets (Table 1). Although the sets were produced under distinctive conditions, they all show that the belly and legs, particularly the front legs, were important landing sites for both species, accounting for 67–98% of all landings; in addition, the flank was important for *G. m. morsitans*. The data obtained by the unexposed observers covered wet and dry seasons and suggested a seasonal effect, with the proportion of *G. pallidipes* on the legs and belly varying significantly between months ($F_{6,623} = 16.7$, $P < 0.001$). In January (wet season), 56% (77/140) of tsetse were observed on

Table 1. Percentage distribution of landings on oxen, in five studies under distinctive conditions, involving observers in pits (unexposed) or beside the oxen (exposed). See Fig. 1 for location of body regions.

	Glossina pallidipes			*Glossina morsitans*	
	Rekomitjie	Rekomitjie	Rekomitjie	Rekomitjie	Makuti
Area	Rekomitjie	Rekomitjie	Rekomitjie	Rekomitjie	Makuti
Observers	Unexposed	Exposed	Exposed	Unexposed	Exposed
Time of day	Afternoon	Afternoon	Morning	Afternoon	Afternoon
No. of individual oxen	8	10	4	8	1
Observation period	Sept 03−April 04	Nov 03−Aug 05*	Jun−August 05	Sept 03−April 04	Jan−March 04
Days observed	112	171	98	112	43
Total sample size	1898	6087	2235	113	1503
Leg, upper front	3.8	12.7	15.1	15	14.3
Leg, middle front	11.1	17.4	23.3	6.2	13.6
Leg, lower front	40.1	14.4	11.6	15	10.7
Leg, upper back	1.4	6.4	4.6	1.8	5.6
Leg, middle back	4.6	10.1	10.9	4.4	5.5
Leg, lower back	9.5	6.3	4.3	0.9	3.4
Belly	27.5	27.4	28.3	23.9	27.9
Flank	1.6	3.0	1.4	31.9	13.6
Other†	0.4	2.3	0.5	0.9	5.3

*Excludes Jan–Apr in all years.
†Head, neck, back, hindquarters and tail.

the legs compared with 39% (54/140) on the belly, whereas in October (hot, dry season) the respective percentages were 80% (550/686) and 19% (130/686).

Data from studies using unexposed observers provides the best means of comparing the landing patterns of *G. m. morsitans* and *G. pallidipes* as the datasets for each species were produced simultaneously. To avoid the possible confounding effects of, say, individual cattle or season, we selected data from only those 10-min observation periods in which both *G. pallidipes* and *G. m. morsitans* were recorded. This produced a subsample of 139 *G. pallidipes* and 113 *G. m. morsitans*, of which 97.8% (136/139) and 67.3% (76/113), respectively, were observed on the legs or belly of cattle ($F_{1,138} = 41.7$, $P < 0.001$ for difference between means).

The distribution of feeding flies, recorded during studies with exposed observers, suggested that feeding sites were even more concentrated than landing sites. This is illustrated by considering the lower front legs, which represent about 1% of the total surface of an ox and where landings were most abundant per unit area. In afternoon countings of *G. pallidipes* at Rekomitjie and *G. m. morsitans* at Makuti, the lower front legs accounted for 14.4% and 10.7% of total landings, respectively (Table 1), as against 21.2% ($n = 6946$) and 17.6% (2756) of total feeds, respectively. However, as it is landing rather than feeding that is responsible for contact with insecticide, it is safer to focus on the distribution of landings.

Treating cattle with insecticide had no significant effect on the duration of landing bouts (Fig. 2). The shape parameter (α) was not significantly different from 1, suggesting that the durations of landing bouts were distributed exponentially, and the mean duration of the bout was 30.3 s (± 0.7 standard error [SE]) which is very similar to the 33 ± 3 s previously reported by Schofield & Torr (2002).

Controls: untreated cattle and whole-body applications

The knockdown rates of *G. pallidipes* and *G. m. morsitans* exposed to untreated control cattle were only 0.98% (118/12 059) and 0.21% (3/1416), respectively. As these percentages were so low, the knockdowns for the various insecticidal treatments were not corrected for the control.

The persistence of the whole-body treatment varied markedly between trials, as illustrated by the knockdowns for trials conducted in August 2002 and January 2003 (Fig. 3a). Monthly plots of the persistence period estimates for the 19 separate trials of the whole-body treatment showed a seasonal pattern, with the period being ~ 1 week in October–February, compared with ~ 4 weeks in June–July (Fig. 3b). This fluctuation is strongly

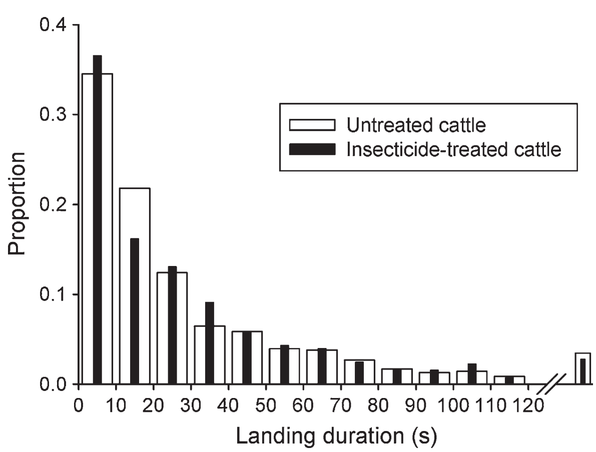

Fig. 2. Frequency of landing bouts for *Glossina pallidipes* feeding on untreated ($n = 1194$) and insecticide-treated ($n = 583$) cattle.

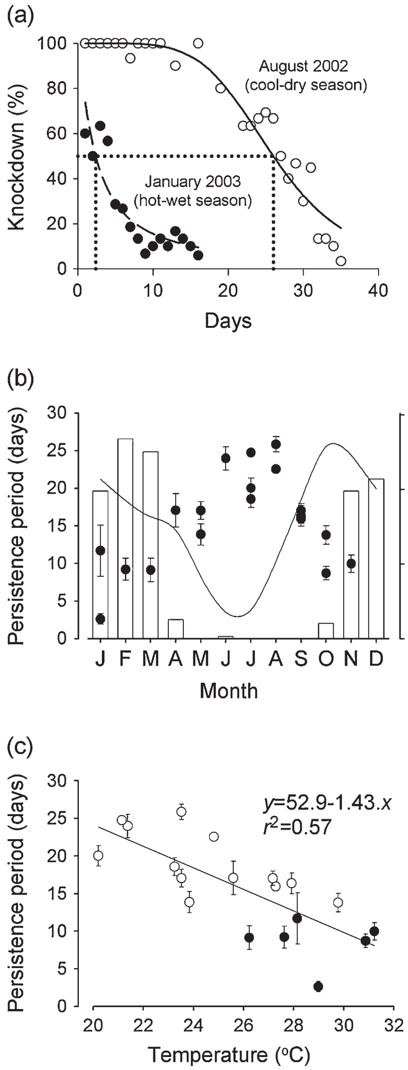

Fig. 3. Seasonal variation in the knockdown of tsetse exposed to cattle sprayed all over with 0.005% deltamethrin. (a) Knockdown of female *Glossina pallidipes* during January (wet season; ● and dashed line) and August (dry season; ○ and solid line); drop-lines indicate the times at which knockdown declined to 50% (persistence period). (b) Estimates of persistence periods (± 95% CI) from 19 separate trials carried out between May 2002 and October 2003 and the mean monthly temperature (solid line) and rainfall (open bars). (c) Scatterplot of persistence periods (± 95% CI) against mean temperature during the trial (dry season, ○; wet season, ●).

correlated with seasonal variation in ambient temperature (Fig. 3c); for every 1 °C increase in temperature, the persistence period decreased by 1.5 days ($r^2 = 0.58$). After allowing for the effect of temperature, rain also decreased the effective life of the insecticide application significantly ($F_{1,16} = 11.4$, $P < 0.01$) with the six shortest persistence periods being in the wet months. Hence, the shortest periods of efficacy are in November–February, which is typically warm and wet in Zimbabwe, whereas the longest periods are in June–July, which is cool and dry (Fig. 3b).

Insecticide-treated cattle: restricted applications

Studies of the landing sites of tsetse suggested the feasibility of a range of restricted application regimes. For instance, virtually all *G. pallidipes* landed on the belly and legs, which represent ~ 20% of the total surface area of an animal; treating just this region would thus reduce insecticide costs by ~ 80%. Even greater savings might be made by treating just the middle and lower front legs, which represents just ~ 2% of the animal's body surface but where ~ 50% of *G. pallidipes* are seen (Table 1). Accordingly, studies were made of the efficacy of five different restricted application regimes where only the following regions were treated: (a) belly and legs; (b) legs; (c) front legs; (d) middle and lower front legs, and (e) lower front legs (Fig. 1). The amount of insecticide applied in each of these regimes was 20%, 10%, 5%, 2% and 1%, respectively, of the amount applied to the whole body. For example, with Spot-On™, which is normally applied at 1 mL/10 kg, a 400-kg ox required only 0.4 mL for the lower front legs only treatment (i.e. 0.2 mL on each leg).

There was no consistent difference in the effective life of Decatix™ and Spot-On™ and, as expected, the persistence of the restricted application regimes varied with season. Both these features can be illustrated by considering three trials where the legs and belly of cattle were treated (Fig. 4). Regression analysis showed that there was no significant difference in the persistence of the restricted Spot-On™ and Decatix™ applications, but these were consistently, and significantly, less than that of the whole-body regime. With this regime, the proportional effect of season was greater than with the whole-body treatment. In the cool season (July), for instance, the persistence period for an animal sprayed with Decatix™ over its entire body was 20 days (95% CI 19–21 days), compared with 16 days (95% CI 15–17 days) for the restricted application. By contrast, in the hot, wet season (February), the respective persistence periods were 9 days (95% CI 8–11 days) and 5 days (95% CI 4–7 days).

The persistence periods for cattle treated with insecticide applied to the legs and belly or legs only varied between ~ 2 and 25 days (Fig. 5). The more restricted applications (i.e. front legs only, middle and lower front legs, lower front legs) had very short persistence periods, with the maximum, from four trials of each regime, being 3 days (95% CI 1.9–3.3 days) for the front legs only, 3 days (95% CI 1–5 days) for the lower front legs only, and 6 days (95% CI 4–7 days) for the front pasterns only. Although the effective lives of these application regimes were very short, the amount of insecticide applied was very small, at just 5%, 2% and 1%, respectively, of that required for the whole-body regime.

The knockdown rates of tsetse landing on treated and untreated regions of the body (Fig. 6) show that for all application regimes, there was a significant knockdown from treated and untreated zones but that knockdown was generally greater for flies from a treated zone. Moreover, as the overall treated area diminished, the knockdown of tsetse caught from the treated and untreated regions declined. Presumably, these trends are due to the movement of insecticide and tsetse from treated to untreated parts of the body. Thus the reduction in efficacy seems to be due to: (a) tsetse landing and feeding on untreated areas, and (b) there being less insecticide on the animal in total.

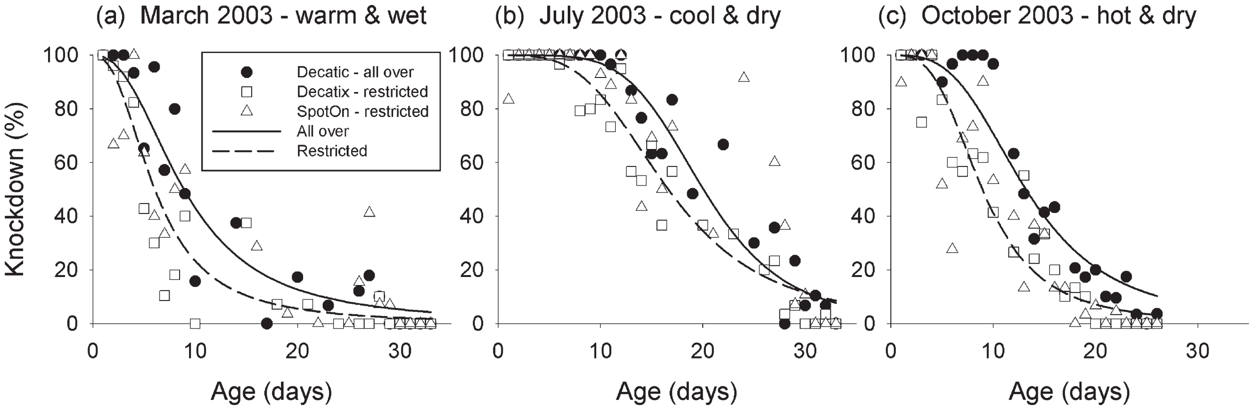

Fig. 4. Knockdown of wild, female *Glossina pallidipes* exposed to cattle treated with deltamethrin (0.005% Decatix™ or 1% Spot-On™) applied either to the whole body or with 20% of the standard dose applied to the legs and belly only. Regression lines fitted to pooled data for Spot-On™ and Decatix™. (a) March 2003, warm and wet; (b) July 2003, cool and dry; (c) October 2003, hot and dry.

High doses of insecticide

The finding that knockdown is reduced for restricted application regimes, even for flies landing on the treated regions, suggested that greater efficacy with the restricted applications might be achieved by increasing the concentration of the formulation applied. Accordingly, studies were made of the knockdown produced by applying Spot-On™, to the middle and lower front legs at five times the normal concentration (i.e. at 10% rather than 2% of the standard whole-body dose).

In one trial conducted in October, the persistence period for the animal treated with the high dose (10%) on the middle and lower front legs was 3 days (95% CI 2–4 days), compared with 1 day (95% CI 0.7–1.6 days) for the standard 2% dose on this zone, and 16 days (95% CI 15–17 days) for the whole-body application. In a second trial conducted over 20 days in July, the persistence period for the high dose on the middle and lower front legs was 8 days (95% CI 6–12 days), whereas the knockdown rate produced by the whole-body treatment was $>$ 90% for the duration of the experiment. These results suggest that increasing the dose of insecticide did not materially improve the efficacy of the restricted application regime.

Low doses of insecticide

The finding that tsetse landing on untreated regions of the body were knocked down when either the pour-on or suspension concentrate had been applied to other regions suggests that the insecticides might spread over the host's body. Hence, the effect of restricted application may be a simple consequence of reducing the amount of insecticide applied, rather than treating particular body regions. To test this hypothesis, we compared the knockdown of tsetse exposed to cattle treated with insecticide applied to (a) the whole body at the standard dose, (b) the whole body at 5% of the standard dose, and (c) the front legs only at 5% of the standard whole-body dose.

The persistence periods of the standard whole-body treatments with Decatix™ ranged between 15 days (95% CI 14–17

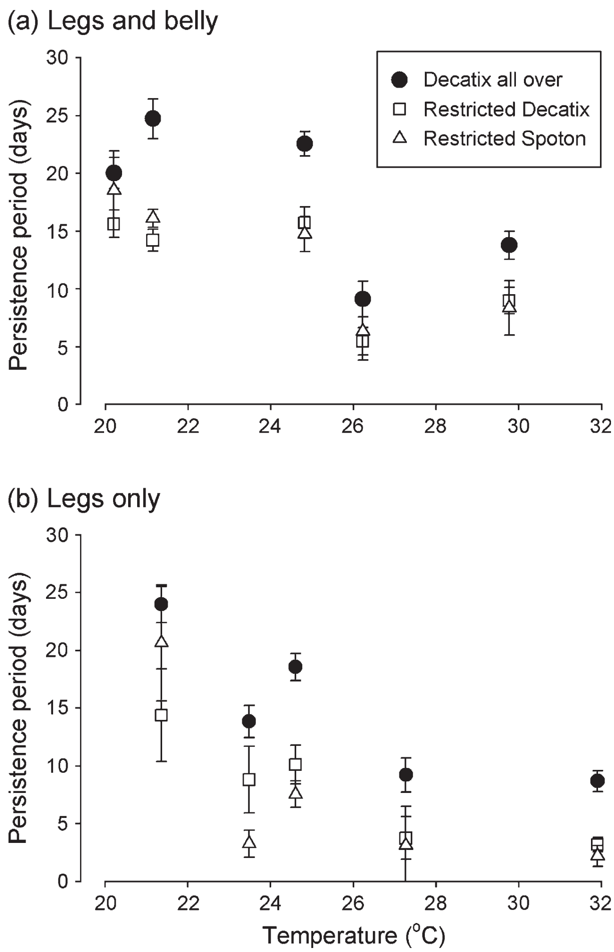

Fig. 5. Persistence periods (days ± 95% CI) for trials of cattle at different mean temperatures after treatment with deltamethrin applied to the whole body or as restricted applications to (a) the belly and legs only, or (b) the legs only.

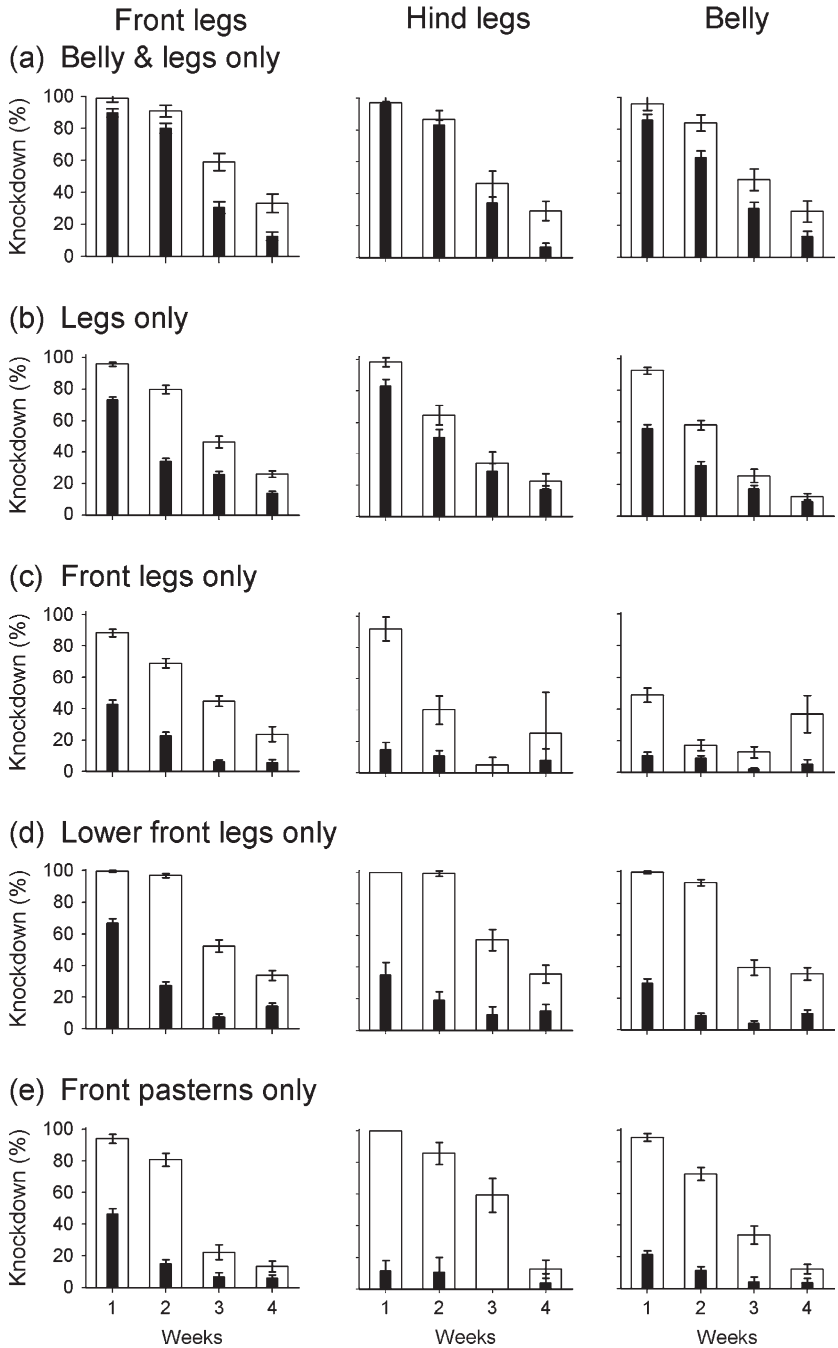

Fig. 6. Knockdown (± standard error) of female *Glossina pallidipes* caught from various body regions of cattle treated with deltamethrin applied either to the entire body (open bars) or to restricted regions (solid bars). Error bars represent largest back-transformed value.

days) and 26 days (95% CI 24–30 days). As expected, the persistence of the restricted (5% applied to the front legs) and low-dose (5% applied to the whole body) treatments were much shorter, with, in some cases, the mean knockdown consistently $< 50\%$. Analysis of the results for the restricted and low-dose treatments only showed that there was a significant effect of the insecticide formulation ($F_{1,93} = 22.0$, $P < 0.001$) and application method ($F_{1,93} = 15.3$, $P < 0.001$) on the percentage knockdown. These effects are illustrated by the percentage knockdown for the first week with each treatment. For cattle treated with Decatix™, the knockdown rate was 99% (286/288) for the standard whole-body treatment, 80% (162/203) for the restricted application, and 50% (123/244) for the low-dose treatment of the whole body. For cattle treated with Spot-On™, the respective percentages were 76% (204/286), 42% (110/264) and 17% (45/259). Decatix™ was sprayed directly onto the whole of the

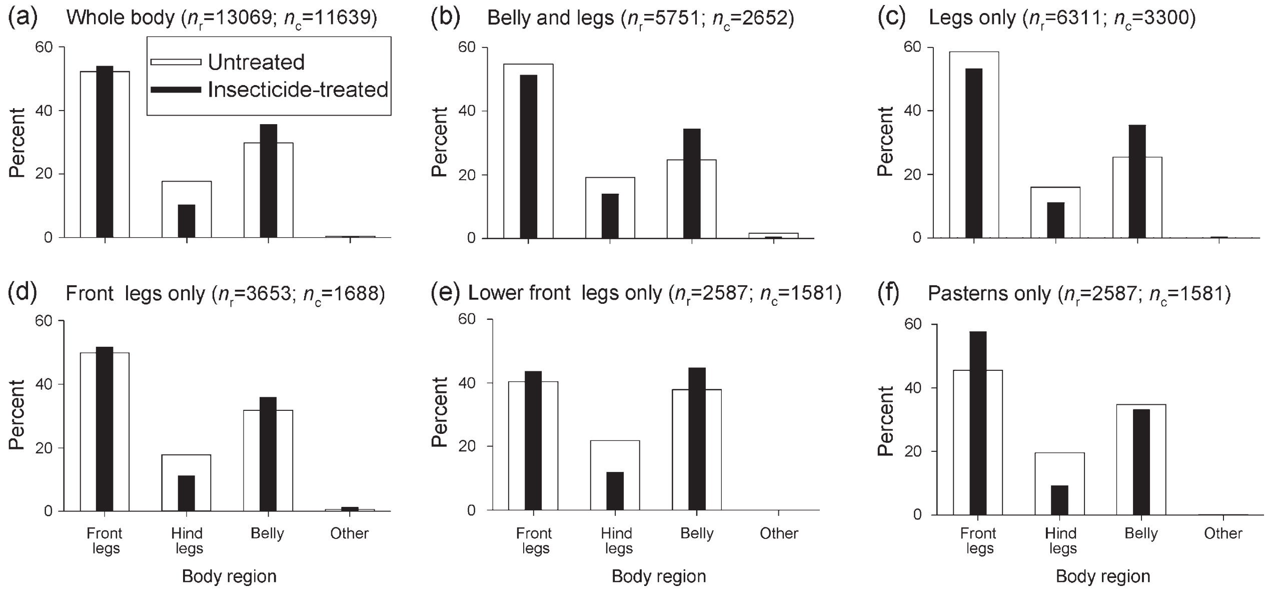

Fig. 7. Distribution of tsetse on untreated (open bars) and insecticide-treated (solid bars) cattle. Numbers of tsetse observed on treated and untreated cattle are n_r and n_c, respectively; n_r includes cattle treated with Decatix™ or Spot-On™ and, hence, is generally twice as big as n_c for each treatment.

restricted surface to be treated, whereas Spot-On™ was applied only to the highest part. Hence, the poorer performance of Spot-On™ in this experiment suggests that it did not spread down with perfect efficiency. This accords with the chemical assays of Vale *et al.* (1999), which showed that Spot-On™ remained most concentrated at the very place it was put.

Effect of pyrethroids on the landing and feeding distributions of tsetse

The numbers of tsetse caught from the front legs, hind legs, belly and other regions during the bioassays indicated whether applying insecticide to one part of an animal caused tsetse to move to another, untreated region.

Pooling all the data for each of the treatments (Fig. 7) did not provide any compelling evidence of a shift from treated to untreated areas. For instance, although treating legs (Fig. 7c) increased the proportion of flies caught on the belly (35.5%) compared with the untreated control (25.4%), the same effect was apparent with the belly and legs (34.4% vs. 24.7%, Fig. 7b) and whole-body treatment (35.5% vs. 29.7%, Fig. 7a). Further, treating the front legs (Fig. 7d) or parts thereof (Fig. 7e, f) did not increase the proportion caught on the hind legs.

Although we found no clear and consistent effect of deltamethrin on the distribution of tsetse, we did observe a marked effect of season. This is most clearly illustrated with the whole-body treatment, which was replicated over a large number of animals and months. The results (Fig. 8) showed that the slight decrease in the proportion of tsetse collected from the legs of insecticide-treated cattle was not significant, but there was a significant ($F_{1,19} = 4.1$, $P < 0.001$) difference in the proportion of tsetse on the legs of the cattle between trials, with the greater proportion during the cool, dry season in general agreement with the results from the direct observation of tsetse landing on cattle (Table 1).

Restricted application regimes for G. m. morsitans

Limited studies to assess whether a restricted application regime was also effective against *G. m. morsitans* were undertaken at Rekomitjie in March 2004, when this species was relatively abundant. As expected from the observations of

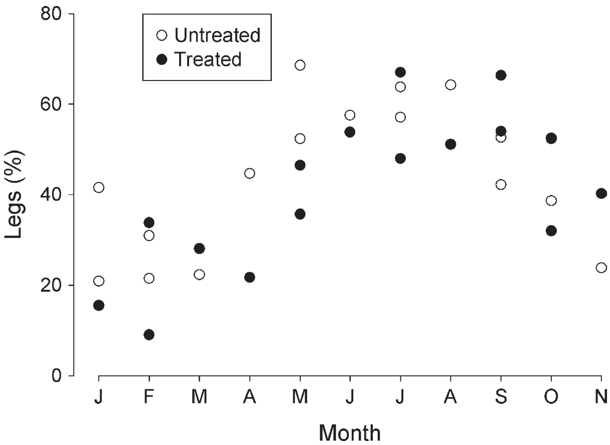

Fig. 8. Percentage of female *Glossina pallidipes* collected from the legs of untreated cattle, or cattle treated with a whole-body application of Decatix™. Percentages based on observation of 135–1040 (mean = 617) insects collected from each test animal.

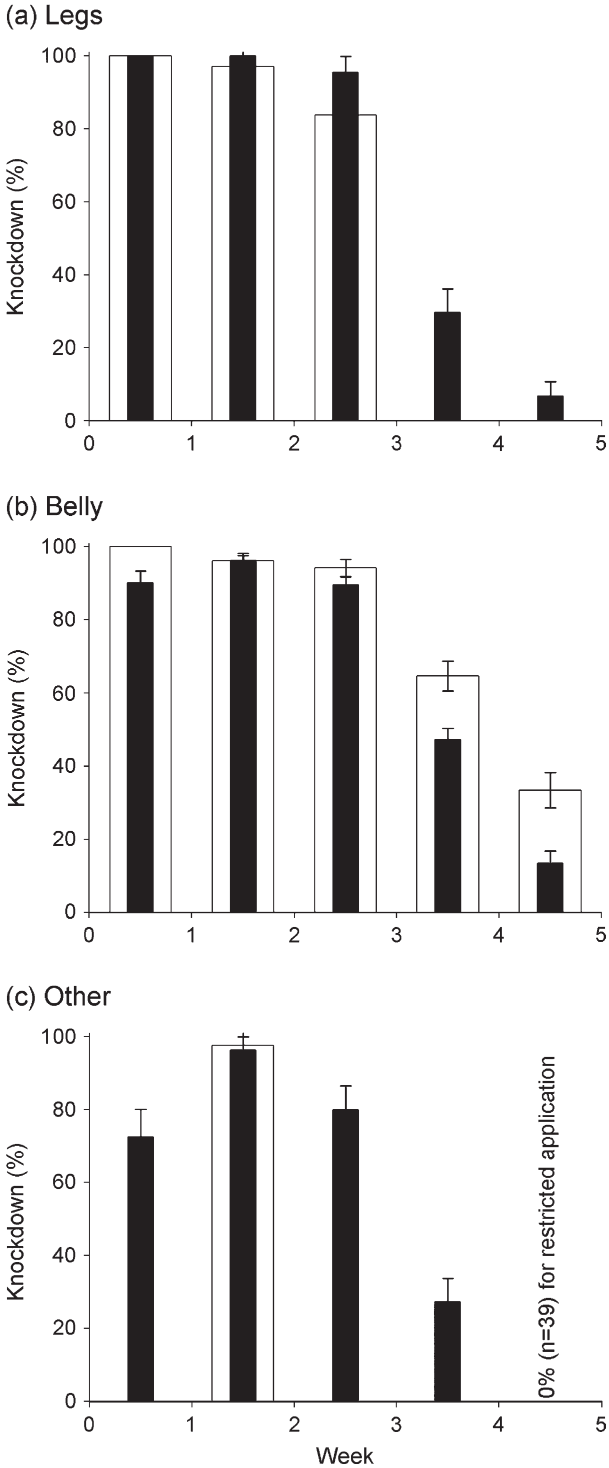

Fig. 9. Knockdown (± standard error) of female *Glossina morsitans morsitans* contacting the (a) legs, (b) belly, or (c) other body regions of cattle treated with deltamethrin applied either to the whole body (open bars) or to the legs and belly only (solid bars). Percentage estimates based on an average sample size of 82 (range 20–267) tsetse and error bars represent largest back-transformed value. Results for whole-body treatment in (a) and (c) are not shown due to low (< 20) sample sizes.

G. m. morsitans landing on untreated cattle (Table 1), a relatively low percentage of tsetse was caught on the legs (339/2206 = 15.4%), whereas high proportions were caught on the belly (1567/2206 = 71.0%) and other (300/2206 = 13.6%) – mainly flank – regions of the test animals.

For the whole-body application, the persistence period was 27 days (95% CI 24–31 days), which is longer than that for *G. pallidipes* at a comparable time of year (Fig. 2). For the restricted applications, there was no significant difference in the performance of the Spot-On™ and Decatix™ formulations, as was the case with *G. pallidipes*, and so the results were pooled. Analysis of these data showed a significant difference between restricted and whole-body applications ($F_{1,225} = 13.4$, $P < 0.001$), but no significant difference in the knockdown rates of tsetse collected from different body regions, irrespective of whether they had been treated with insecticide or not (Fig. 9). The persistence period for the restricted application was 22 days (95% CI 20–25 days), which, as with the whole-body application, is longer than the persistence period for *G. pallidipes* at a comparable time of year (Figs 3 and 4).

Discussion

Feeding behaviour of tsetse

As with earlier studies, the present work showed that most tsetse landed on the legs and belly of cattle (Torr & Hargrove, 1998; Vale *et al.*, 1999). This concentration of landings was particularly marked for *G. pallidipes,* for which ~ 70% were on the legs, ~ 25% on the belly and < 5% on the rest of the body. For *G. m. morsitans,* the percentage on the legs was slightly smaller (~ 50%) and that on the rest of the body, particularly the flanks, was bigger (~ 20%). Also in accordance with previous studies (Vale *et al.*, 1999) there was a seasonal variation in the feeding patterns of *G. pallidipes,* with ~ 60% of tsetse landing on the legs in May–September compared with ~ 30% during November–March. Several factors might contribute to these seasonal effects; for example, biting flies other than tsetse (e.g. *Stomoxys* spp., *Tabanus* spp.) are more abundant during the wet season (November–March) (Torr & Mangwiro, 2000) and, like tsetse, concentrate on the lower legs and belly (Phelps & Holloway, 1990; Lysyk, 1995) of cattle. Perhaps the host's defensive behaviour against these flies (Torr & Mangwiro, 2000; Schofield & Torr, 2002) disturb tsetse on the legs and hence increase the proportion on the belly. The legs of cattle may, at times, be muddy during the wet season and this may also have deterred tsetse from landing there. Nonetheless, although there were clear and consistent seasonal and interspecific differences in landing patterns, the majority of tsetse always landed on the legs and belly.

Reducing the cost of tsetse control

Restricting the application of insecticide to those regions where most tsetse land can significantly reduce the amount of insecticide required, but it also reduces the effective life of the treatment. For instance, treating only the belly and legs of cattle, where > 95% of *G. pallidipes* landed, reduced insecticide costs by 80% but, at an average temperature of 25 °C, the persistence period for the restricted application was ~ 10 days compared with ~ 15 days for the whole-body regime.

From a practical point of view, it is more useful to consider average percentage knockdown rates over equivalent periods. Using the regression equations from trials conducted in the cool, dry season (August 2004; average mean temperature 24.8 °C), the average knockdown over 28 days was 78%, compared with 57% for the restricted (belly and legs) regime. Thus, whereas the ratio of insecticide costs for the restricted and whole-body regimes is 1 : 5, the benefit ratio is 0.57 : 0.78, so that the benefit-adjusted reduction in cost is 73% rather than 80%. However, if we consider shorter re-treatment periods, the benefit ratio of the restricted application regime improves: at fortnightly intervals the ratio is 0.93 : 0.99 and at weekly intervals the ratio is 1 : 1. Hence, the economic benefits of using a restricted application regime are greater as treatment intervals become shorter.

For *G. pallidipes* and *G. m. morsitans*, the effective life of the whole-body treatment was 1–4 weeks. This accords well with the results of Vale *et al.* (1999), but contrasts with those of Bauer *et al.* (1992), who reported that knockdown of *Glossina palpalis gambiensis* in Burkina Faso exceeded 65% for 75 days after treatment with Spot-On™. The longer effective life of Spot-On™ in Burkina Faso may be because Bauer *et al.* (1992) used teneral (i.e. newly emerged) male and female flies in their studies, whereas we used wild, mature females; there is evidence that tolerance to insecticides is greater in female and older flies (Haddaway *et al.*, 1976; Riordan & Gregory, 1985), although this may be counterbalanced by indications that morsitans-group tsetse are more susceptible than palpalis-group flies (Hadaway *et al.*, 1976). A more likely explanation is that the cattle used in Burkina Faso were more sheltered than at Rekomitjie. Bauer *et al.* (1992) used cattle that were either 'maintained away from sunlight' or exposed to 3 h of sunlight every other day. This modest exposure reduced the effective life of the insecticide significantly, with, for example, the exposed animal producing a mean knockdown rate of 40% at 81–103 days post-treatment compared with 64% for the sheltered animal. In the present study, all animals grazed in woodland surrounding Rekomitjie for ~ 8 h/day and at other times were kept in outdoor pens. Insecticide deposits on the Zimbabwe cattle were therefore exposed not only to sun and rain but also to the abrasive effects of walking through vegetation. This degree of exposure is typical for cattle kept in most tsetse-affected areas.

Currently, the high cost of insecticide means that poor livestock keepers often treat their cattle infrequently. In the Konso district of southern Ethiopia, for instance, farmers aim to treat their cattle with Spot-On™ four times per year (S. Torr, unpublished data). The average knockdown rate produced by an animal treated at these intervals would be just 27%. If, however, they treated the legs and belly of cattle at monthly intervals, the average knockdown rate would be more than doubled, to 57%, and insecticide costs would be reduced by 40%. Even better levels of control would occur if farmers treated their cattle at, say, 3-week intervals. In this case, insecticide costs would still be less than those of the current (whole-body) regime but the average knockdown rate would be nearly tripled, to 73%. Three-fold improvements in the mortality imposed on a tsetse population can have a profound impact; killing 1% of the female population per day would reduce a population by 99% over the course of a year, whereas a 3% reduction would result in a reduction of 99.99% (Vale & Torr, 2004). Thus the restricted application regime would not only allow farmers to reduce costs but also enable them to achieve far better levels of control.

Reducing the intervals between treatments increases efficacy but also increases costs. What is the optimal interval? If we wish to achieve at least the same level of control as that produced by treating the whole body at monthly intervals (average knockdown 78%) then we might treat the belly and legs at fortnightly intervals (average knockdown 93%) or the legs only at weekly intervals (average knockdown 81%). Both the restricted regimes would reduce the annual costs of insecticide by 40%. In practice, treating the belly and legs at fortnightly intervals seems the more robust strategy as the proportion of tsetse on the legs varies with season and between species.

Recently, the cost of pyrethroids has declined drastically, largely because patents have expired. For example, Barrett (1997) calculated that the annual cost of insecticide to treat a whole animal at 14-day intervals in Zimbabwe was Z$7.31/animal/year, equivalent to about US$3/animal/year at the 1990 rate of exchange (Budd, 1999). Vale & Torr (2005) estimated the cost of insecticide for the same treatment regime was ~ US$1/animal/year. Treating just the legs and belly would reduce this to ~ US$0.20/animal/year, which is substantially less than the cost of trypanocides. Even after allowing a generous 10-fold increase in costs to cover import duty, equipment and labour for spraying (Vale & Torr, 2005), the annual cost of treating an animal is just US$2, which is still comparable with the cost of a single treatment with a trypanocide (Shaw, 2004).

The pour-on formulation uses about three times as much insecticide as the spray, but there is little difference in efficacy. It therefore seems that unless access to water or the cost of spraying equipment is prohibitive, the spray formulation is the cheaper option.

Wider implications

The restricted application of insecticide to cattle will not only improve the cost-effectiveness of tsetse control but also has three important implications for other aspects of livestock health and productivity.

Firstly, poorer communities in Africa generally keep indigenous breeds of cattle, which are resistant to several tick-borne diseases. This resistance depends on young cattle being bitten by infected ticks (Acari: Ixodidae) and developing immunity thereafter. This condition, termed enzootic stability, can be undermined by widespread and frequent treatment of cattle with pyrethoids for tsetse control (Van den Bossche & Mudenge, 1999; Eisler *et al.*, 2003). However, the attachment sites of ticks and feeding sites of tsetse differ (Walker, 1974; Torr & Hargrove, 1998; Wanzala *et al.*, 2004) and > 95% tsetse feed on adult cattle (Torr *et al.*, 2001). Thus, by treating only the legs and bellies of older cattle, effective tsetse control might be achieved while reducing the threat to enzootic stability.

Secondly, previous studies have shown that treating cattle with pyrethoids can have a significant impact on the invertebrate fauna involved in breaking down cattle dung (Vale & Grant, 2002; Vale *et al.*, 2004). This has potentially serious implications for those production systems where cattle dung plays an important role in maintaining soil fertility. However, the effect on dung fauna is largely obviated by restricting insecticide to the legs and belly (Vale *et al.*, 2004; G. Vale, unpublished data). Thus the restricted regime is not only cheaper and more effective, but also has a much reduced environmental impact.

Thirdly, it is striking that many, if not most, cattle-feeding Diptera land on the legs. The restricted application of insecticide may therefore also be appropriate as a means of controlling other fly-borne diseases of livestock and, possibly, humans; insecticide-treated cattle have been used to control malaria in Asia (Rowland *et al.*, 2001) and may also be appropriate for controlling malaria transmitted by *Anopheles arabiensis* Patton (Diptera: Culicidae) in Africa (Habtewold *et al.*, 2004).

The present results do not make the use of insecticide-treated cattle a panacea for trypanosomiasis. The method cannot be used where cattle are absent and hence would not have been suitable for eliminating tsetse from a national park such as the Okavango Delta in Botswana (Kgori *et al.*, 2006). Even within farming areas, the distribution of grazing and water, and various aspects of livestock management practices, may lead to a patchy distribution of insecticide-treated cattle and hence prevent effective control of tsetse (Hargrove *et al.*, 2002). Nonetheless, in most situations where trypanosomiasis is a problem, cattle will be present and the restricted application of insecticide, used either alone or in combination with other methods, promises many practical and economic advantages. There is an urgent need to test this in practice.

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