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The magnitude of site and time interaction effect in tsetse fly (Diptera: Glossinidae) trap catches

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Abstract

Site and time effects are important factors determining trap catches of tsetse flies. These factors may interact significantly and therefore confound interpretation of time series data used for population monitoring. We therefore investigated the magnitude and importance of site × time interactions in trap catches of *Glossina pallidipes* Austen and *G. longipennis* Corti using a 2200 trap-days (400 trap-months) data set. The interaction was found to be significant ($P < 0.05$) in 46–100% of the combinations of different numbers of months and sites between 2 and 12. The mean percent variance due to the interaction ranged between 4% and 28% for *G. pallidipes* and 12% and 36% for *G. longipennis*. The interaction was usually less important than the effect of site alone but more important than the effect of time alone. These results suggest that tsetse researchers should examine critically the adequacy of existing approaches to population monitoring with traps and to testing new traps and odour baits.

Introduction

During the last 25 years, the control of tsetse flies (*Glossina* spp., Diptera: Glossinidae) has been facilitated greatly by the development of efficient, attractive devices baited with odours (Vale, 1993; Green, 1994). For example, insecticide-impregnated blue and black cloth targets are now in widespread use for the control of savannah tsetse; a variety of traps and targets are also being used for the control of riverine species. In many control projects, catches from traps are used as convenient indices for monitoring the impact on tsetse populations (Leak *et al*., 1995). Trap catches, however, reflect only apparent and not absolute densities, and are reliable only if sample sizes are quite large (Williams *et al*., 1990a). Trap catches are prone to many biases and, hence, fluctuate in space and time (Morris & Morris, 1949; Glasgow & Duffy, 1961; Smith & Rennison, 1961; Hargrove & Vale, 1978; Dransfield, 1984; Brightwell *et al*., 1987; Williams *et al*., 1990a). More importantly, the two factors, space and time, may interact significantly thereby confounding the main effects of the factors. In such an event, the interpretation of time series data used for population monitoring may be highly distorted. Despite these pitfalls, traps and the indices they generate are still the most popular method for monitoring tsetse populations.

This important issue of the interaction of space and time in tsetse data has never been addressed empirically by tsetse researchers. Similarly, there have been no attempts to investigate combinations of sites and times which might mitigate the impact of interaction effects. In general, researchers appear to have simply designed population monitoring experiments based on logistical constraints, rather than on an informed statistical basis. We therefore took advantage of tsetse monitoring data from Nguruman, Kenya to determine the conditions under which interaction effects might be important. Here, we report results for two tsetse, *Glossina pallidipes* Austen and *Glossina longipennis* Corti (Diptera: Glossinidae), and provide general comments on future needs in experimental design for tsetse field research.

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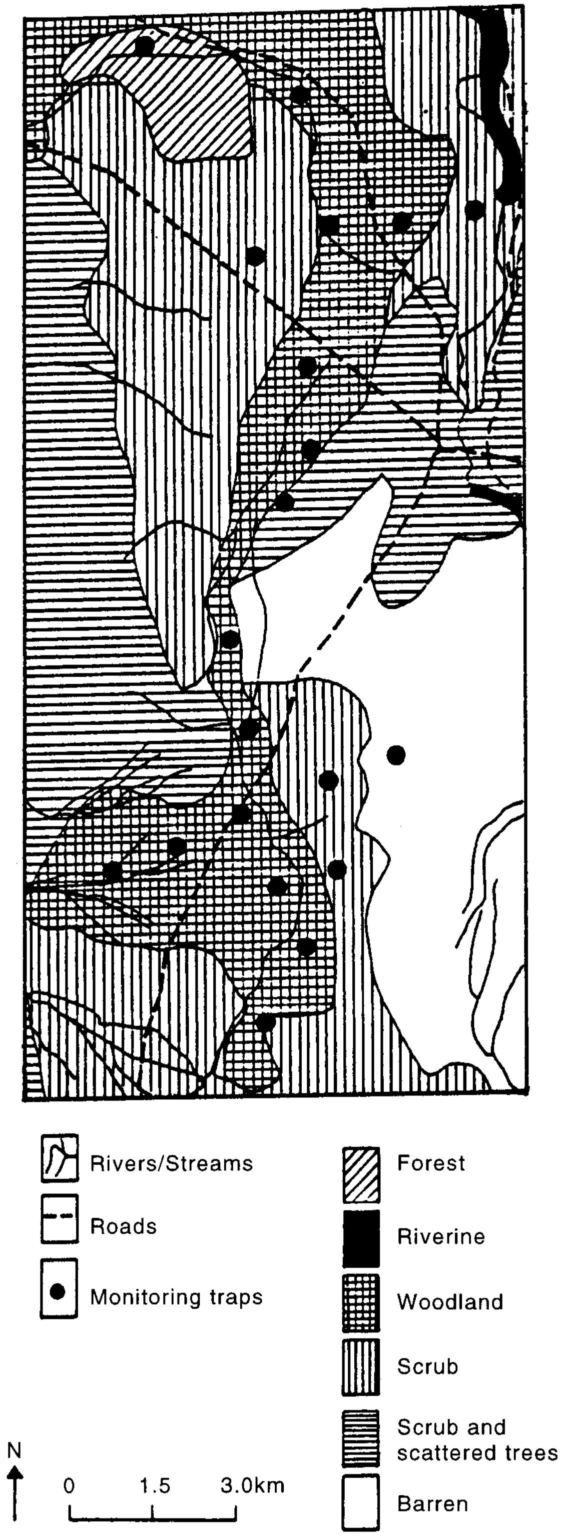

Fig. 1. Map of the study area at Nguruman, Kenya showing the 20 trapping sites.

Table 1. Mean square (MS), expected mean squares (EMS) and variance component estimators (VC).

Source	MS	EMS	VC
Month	M	$\sigma^2_\varepsilon + r\sigma^2_{MS} + s\sigma^2_D + rs\sigma^2_m$	(M–D–I–E)/rs
Days within month	D	$\sigma^2_\varepsilon + s\sigma^2_D$	(D–E)/s
Site	S	$\sigma^2_\varepsilon + r\sigma^2_{MS} + rm\sigma^2_S$	(S–I)/rm
Interaction	I	$\sigma^2_\varepsilon + r\sigma^2_{MS}$	(I–E)/r
Residual	E	σ^2_ε	E

s = number of sites, m = number of months and r = average number of days within each month.

Materials and methods

Field data

The study was conducted at Nguruman (1°50'S; 36°05'E) in Kajiado District, Kenya, in the tsetse suppression area described by Dransfield *et al.* (1990). Between May, 1993 and December, 1994, *G. pallidipes* and *G. longipennis* were captured in NG2G traps (Brightwell *et al.*, 1991), baited with cow urine (*c.* 100 mg/h) and acetone (*c.* 150 mg/h) placed 30 cm behind the trap. Sampling was monthly at 20 fixed sites (geopositioned, fig. 1) for five to seven consecutive days during each of the twenty months. This gave 110 days and a total data set of 2200 trap-days. The distance between any two adjacent traps ranged from 786 to 2954 metres. Trap catches were collected at 24 h intervals and then counted by sex and species. Catch/trap/day ranged between 0 and 2281 for *G. pallidipes* and between 0 and 280 for *G. longipennis* depending on the month of the year.

Data analysis

One hundred and twenty-one combinations of different numbers of sites and months ranging from 2 to 12, were obtained from the data set. Given a combination of s sites and m months, the total number of possible choices from the data set is ${}^{20}C_s \times {}^{20}C_m$, where ${}^{x}C_y = x!/(y!(x-y)!)$. For each combination, 20,000 samples were randomly selected from the possible choices and analysed. The days within any selected month served as replication points to allow for the estimation of the site × month interaction effect. We employed the following model for the analysis of variance (ANOVA) of each of the 20,000 samples in each of the 121 combinations:

$$y_{(i)jk} = \mu + m_i + d_{j(i)} + s_k + ms_{ik} + \epsilon_{(i)jk}$$

where $y_{(i)jk}$ is the catch/trap/day, μ is the general mean, m_i is the effect of month, $d_{j(i)}$ is the effect of days within a month, s_k is the effect of site, ms_{ik} is the month × site interaction effect, and $\epsilon_{(i)jk}$ is the corresponding residual.

A random model was assumed regarding the selected months, days within a month and sites as representative samples from their respective populations. This assumption is reasonable since the months and sites were randomly selected for each sample. Whereas the assumption may not be valid in the case of the days-within-month effect, it is required to enable the quantification of the variation due to this factor. The analysis was carried out for males, females and total catches separately, for each of the two tsetse species *G. pallidipes* and *G. longipennis*. The catch data were transformed to $\log_{10}(x+1)$ scale before analysis.

For each ANOVA, the percentage variance component (%VC) attributed to each of the model's effects was estimated using the expected mean squares (EMS) shown in table 1. The EMS were obtained using the method stated by Hicks (1973). Negative %VC values were equated to zero (Swallow & Monahan, 1984). The mean %VC over all the 20,000 samples was obtained for each combination of months and sites.

To measure the importance of the interaction effect (RI) relative to each of the main effects, the mean interaction %VC was divided by the %VC due to each of the main effects. These are denoted as RI/S and RI/M for the importance of the interaction effect relative to site and month effects respectively. A value greater than unity implied that the interaction effect was more important than the main effect.

For each combination of months and sites, the percentage number of times out of the 20,000 samples in which the ANOVA effect was significant at $P \leq 0.05$ level was calculated.

Results

Statistical trends for females and males were similar (table 2). Hence, only results for the total catch are presented in the figures. Figure 2 shows the percentage number of times out of 20,000 samples in which the interaction effect was significant.

Generally, the percentage of significant interaction effects increased as the number of sites and months increased. For *G. pallidipes* the percentage varied between 59% and 100% for the different combinations of sites and months. The corresponding range for *G. longipennis* was 46%–100%. Hence, interaction effects were significant at least half of the time, regardless of number of sites and months chosen. The percentage number of significant interaction effects increased more rapidly with an increase in months rather than sites. For example, given three sites and five months, the percentage, with respect to *G. pallidipes* was 96, whereas, given five sites and three months, the percentage was 80. The corresponding values for *G. longipennis* were 91% and 78%, respectively. For *G. pallidipes*, the incremental increase was as high as 22 or 23 for a unit increase in the number of sites or months. The corresponding values for *G. longipennis* were 22 or 26. As the number of sites or months increased, these increments approached zero. With a combination of more than six sites and three months, nearly 100% of the interaction effects were significant for both species.

The mean %VC due to the interaction is presented in fig. 3. The minimum and maximum values are presented in table 2. The mean %VC due to the interaction term ranged between 4% and 28% for *G. pallidipes* and between 12% and 36% for *G. longipennis*. For *G. pallidipes*, a combination of more than five or seven months and any number of sites limited the interaction effect to at least 10% or 20% of the total variation respectively. With only two or three sites, the interaction %VC was always above 17% for *G. pallidipes*. The interaction effect was more pronounced for *G. longipennis* with the %VC as high as 28% or 36% for a combination of six or eight months with any number of sites, respectively. Also, with only two or three sites, the interaction %VC was at least 20% for *G. longipennis*.

The importance of the interaction effect relative to site effect (RI/S) ranged between 0.04 and 0.88 for *G. pallidipes*, (fig. 4a) and between 0.26 and 2.0 for *G. longipennis* (fig. 4b). It generally decreased with an increase in the number of sites while increasing with an increase in the number of months. The importance of the interaction effect relative to month effect (RI/M) was in most cases greater than unity or very close to unity for all combinations of sites and months as well as for both species. It ranged between 0.84 and 7.8 for *G. pallidipes* (fig. 5a) and between 11 and 26 for

Table 2. Minimum and maximum mean percent variance component (±SE) due to the difference sources of variation (n = 20,000).

Source of variation		Male	Female	Total
G. pallidipes				
Site	maximum	81.4 ± 0.05	84.8 ± 0.04	85.2 ± 0.04
	minimum	25.0 ± 0.19	27.4 ± 0.19	27.3 ± 0.19
Month	maximum	31.4 ± 0.15	28.4 ± 0.14	29.3 ± 0.15
	minimum	3.7 ± 0.02	0.3 ± 0.003	0.5 ± 0.004
Interaction	maximum	32.5 ± 0.08	29.0 ± 0.08	28.4 ± 0.08
	minimum	5.1 ± 0.02	4.0 ± 0.01	3.5 ± 0.01
Days within month	maximum	8.1 ± 0.08	11.9 ± 0.11	13.3 ± 0.10
	minimum	0.7 ± 0.004	1.4 ± 0.01	1.3 ± 0.01
Residual	maximum	20.4 ± 0.09	18.2 ± 0.08	18.0 ± 0.08
	minimum	6.9 ± 0.01	6.5 ± 0.01	6.2 ± 0.01
G. longipennis				
Site	maximum	47.1 ± 0.04	37.4 ± 0.04	48.4 ± 0.04
	minimum	16.4 ± 0.14	12.4 ± 0.10	15.7 ± 0.14
Month	maximum	25.5 ± 0.11	24.7 ± 0.09	25.9 ± 0.11
	minimum	0.5 ± 0.01	0.9 ± 0.01	0.7 ± 0.01
Interaction	maximum	35.0 ± 0.10	33.1 ± 0.05	36.2 ± 0.07
	minimum	11.4 ± 0.06	13.7 ± 0.06	11.8 ± 0.06
Days within month	maximum	12.4 ± 0.08	9.5 ± 0.07	15.2 ± 0.08
	minimum	1.7 ± 0.01	1.3 ± 0.01	2.3 ± 0.01
Residual	maximum	38.3 ± 0.11	34.0 ± 0.16	33.5 ± 0.10
	minimum	23.7 ± 0.04	35.6 ± 0.02	21.1 ± 0.04

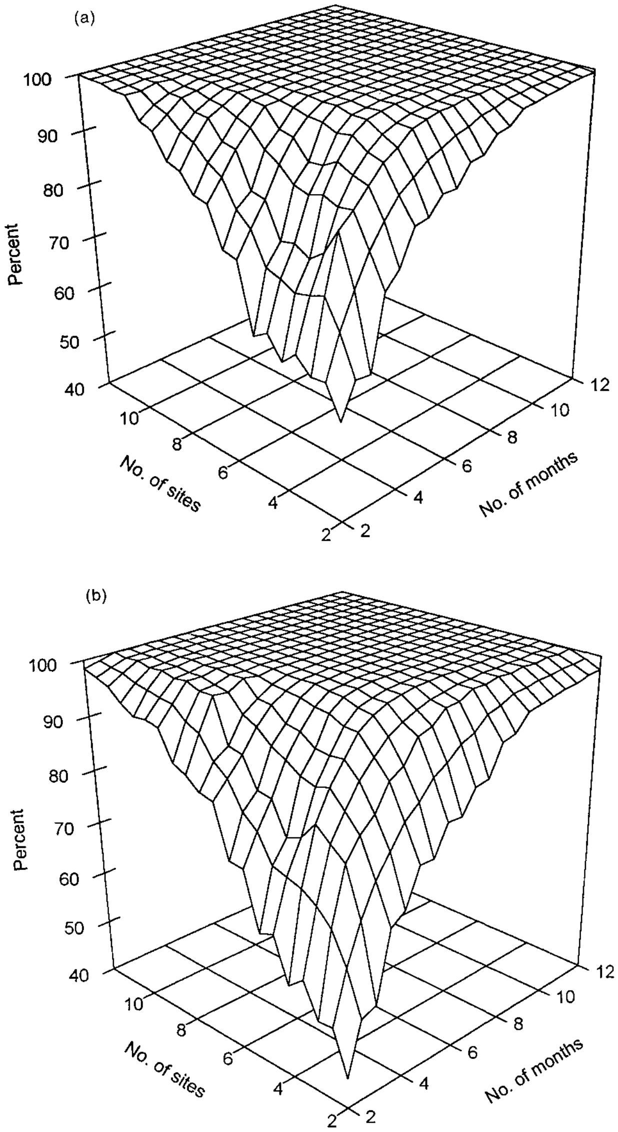

Fig. 2. Percent number of times out of 20,000 samples when the interaction effect of site and month was significant at $P \leq 0.05$ for total (a) *Glossina pallidipes* and (b) *G. longipennis* catches.

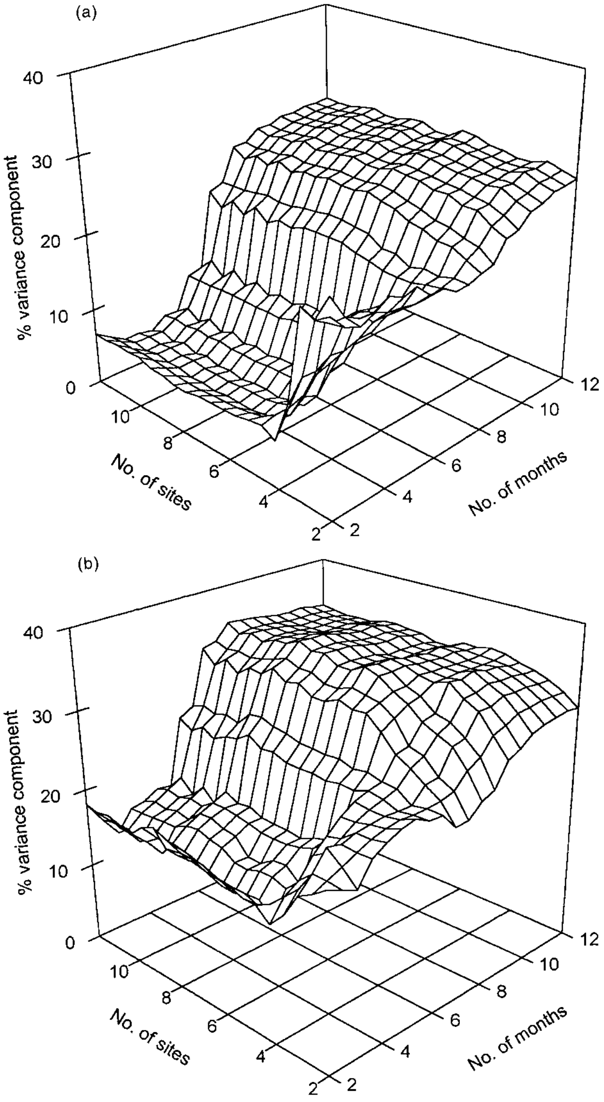

Fig. 3. Mean, over 20,000 samples, of the percent variance component accounted for by the interaction effect of site and month for total (a) *Glossina pallidipes* and (b) *G. longipennis* catches.

G. longipennis (fig. 5b), generally increasing with an increase in number of sites but decreasing with an increase in the number of months. These trends indicate clearly that the interaction effect is more important than the time effect, while being about as important as the site effect as a source of variation.

Discussion

The trap catch data analysed in the studies reported here are typically used by researchers for the monitoring of changes in tsetse population densities. This study has shown that the interaction effect between sites and months is of considerable importance in the interpretation of population data for both *G. pallidipes* and *G. longipennis*. In simple terms, this means that trap catches at fixed sites may not behave in a consistent manner over months, e.g. catches may increase in one area while going down in another area. These interaction effects have unknown origins, but are most likely related to climatic changes, which affect flies indirectly through changes in vegetation structure and host dispersion. Tsetse populations are known to concentrate in certain vegetation types in different seasons, confounding estimates of global density (Hargrove & Vale, 1980; Hargrove, 1981). At Nguruman, tsetse concentrate in specific areas in different seasons (Brightwell *et al.*, 1992). When it is hot and dry, they retreat into areas of thick vegetation near water; when it is cooler and wetter, they are more evenly distributed in woodlands and thickets. These gross spatial trends, along with a probable change in activity and mean daily displacement, confound interpretation of relative trap catches over time (Williams *et al.*, 1990b). Since traps

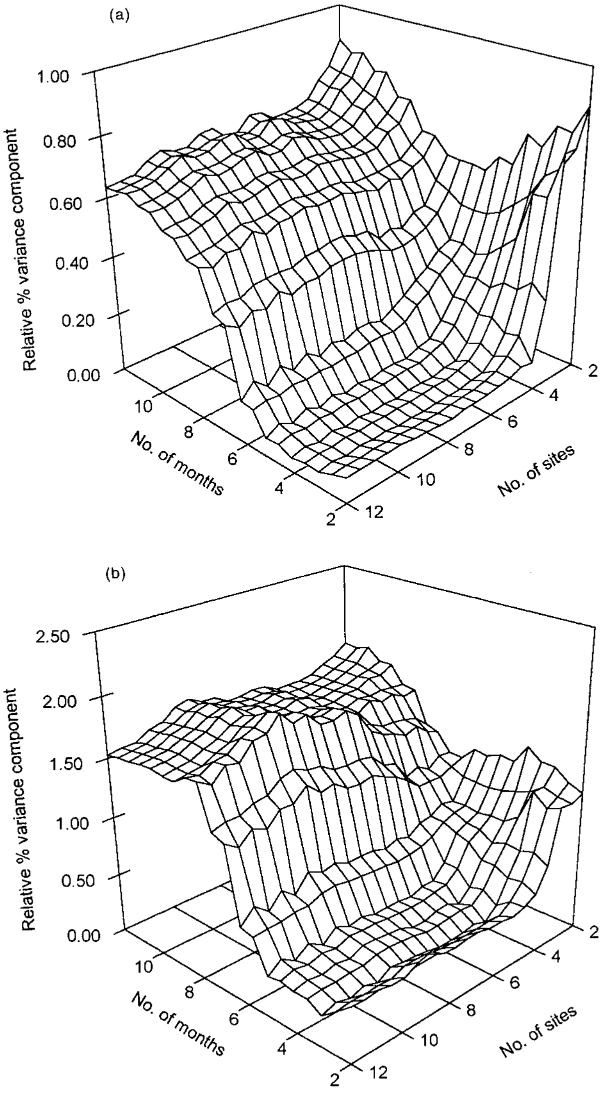

Fig. 4. The importance of site×time interaction effect relative to site effect, as measured by the ratio of the percent variance component attributed to the two effects, for total (a) *Glossina pallidipes* and (b) *G. longipennis* catches. (Note: axis orientation is different from those of other figures for better viewing).

themselves also vary in efficiency with temperature, light, etc. (Vale & Hargrove, 1979; Williams *et al*., 1990b; Brightwell *et al*., 1991), seasonal changes in capture efficiency can result in numerous pitfalls of interpretation. If trap indices are to be used for reliable population estimation, then sample sizes must necessarily be generated over the longest possible period (Williams *et al*., 1990a), and habitat heterogeneity must be considered. In practice, few researchers are able to meet these requirements, and hence they generate only crude population data.

Our study revealed that the effect of days within months was usually the least important source of variation. This may be due to the fact that the days within each month were consecutive and not random. Hence, the effect of the interaction between sites and days will

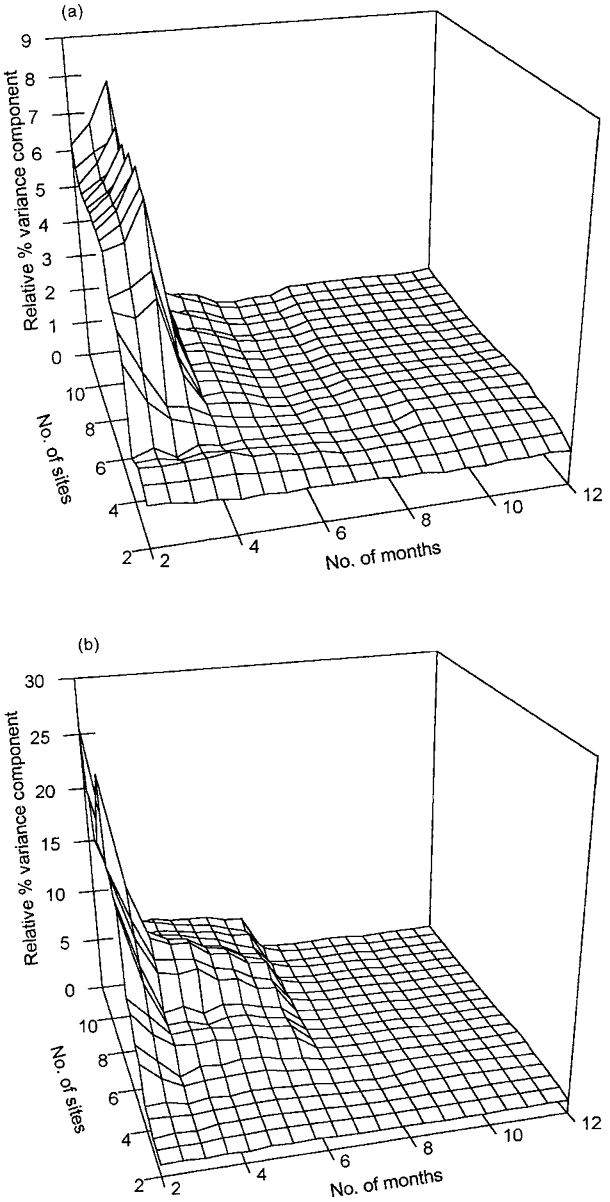

Fig. 5. The importance of site×time interaction effect relative to month effect, as measured by the ratio of the percent variance component attributed to the two effects, for total (a) *Glossina pallidipes* and (b) *G. longipennis* catches.

probably be much less than that of the interaction between sites and months. However, since the results of the field experiments are expected to be applicable at all sites within the study areas, as well as in all months, seasons and years, the importance of the interaction may be underestimated.

In conclusion, we recommend that tsetse researchers critically examine the adequacy of existing sampling efforts for population monitoring. We believe effort should be put into developing better alternative for this purpose. A promising approach is to use a stratified, rather than a conventional simple random, sampling method for tsetse population monitoring.

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