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Autor:	Tarimo, S.A. / Snow, F.W. / Butler, L.
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¹ The International Centre of Insect Physiology and Ecology, Nairobi, Kenya

² 11, Newland Road, Banbury, Oxon, OX16 8HQ, England

³ West Virginia University, Entomology Department, Agriculture Science Building, Morgantown, West Virginia 26505, USA

The probability of tsetse acquiring trypanosome infection from single blood meal in different localities in Kenya

S. A. TARIMO¹, F. W. SNOW², L. BUTLER³, R. DRANSFIELD¹

Summary

The probability of tsetse, *Glossina pallidipes*, acquiring a trypanosome infection from a single blood meal was estimated in five localities on the Kenya coast which were selected for differences in habitat and host availability. The probability that one blood meal contained infective *Trypanosoma congolense* was 0.0077 in rural areas with domestic animals, 0.0019 in extensive areas of natural habitat with wild hosts and 0.0013 in an area with domestic animals under regular chemoprophylaxis. The respective probabilities for *T. vivax* were 0.0010, 0.0024 and 0.0021.

Key words: *G. pallidipes*; tsetse; Kenya; trypanosomiases; epizootiology; challenge.

Introduction

The level of trypanosomiasis transmission can be regarded as being influenced by five parameters: fly density, feeding frequency, feeding behaviour, the probability of a tsetse picking up an infection from a single blood meal and of maintaining the infection long enough to infect an animal (Rogers, 1979a). This paper concentrates on one of these factors; the probability of tsetse picking up an infection. This has only been estimated for *G. swynnertoni* in Tanzania (Rogers and Boreham, 1973).

It has been observed that not all infected blood meals give rise to infection in tsetse (Fairbairn and Watson, 1955; Elce, 1971). When the infection rates of

Correspondence: Dr. S. A. Tarimo, The International Centre of Insect Physiology and Ecology, P.O. Box 30772, Nairobi, Kenya

the hosts are also known and the tsetse are feeding on a few host species, the barrier to infection from host to tsetse can also be assessed (Rogers, 1979b).

The probability that a female *G. pallidipes* will pick up an infection from a single blood meal has been estimated in five localities along the Kenya coast (see under Study area, below). In one locality where the animals were also sampled for trypanosome infection, the barrier to infection was also estimated.

Materials and Methods

Study area

Shimba Hills and Mwalewa ($4^{\circ}5'$ S, $39^{\circ}25'$ E, alt. 180 m and $4^{\circ}34'$ S, $39^{\circ}08'$ E, alt. 75 m, respectively) are areas of forest and bushed grassland. Only wild animals were present in this area, and these included bushbuck (*Tragelaphus scriptus*), bushpig (*Potamochoerus porcus*), warthog (*Phacochoerus aethiopicus*), and buffalo (*Syncerus cafer*). Diani ($4^{\circ}15'$ S, $39^{\circ}34'$ E, alt. 15 m), Ukunda ($4^{\circ}26'$ S, $39^{\circ}35'$ E, alt. 12 m), and Muhaka ($4^{\circ}20'$ S, $39^{\circ}32'$ E, alt. 35 m) were forest relicts in rural areas and had both domestic and wild animals present. Cattle, sheep and goats were under regular use of chemoprophylaxis (isometamidium chloride) at Diani. Occasional warthog, bushpig, bushbuck, duiker (*Cephalophus* spp.) and suni (*Nesotragus moschatus*) were also present. These study areas have been described before in detail (Tarimo et al., 1984).

Sampling and dissection techniques and infection rate in animals

The blue biconical trap (Challier and Laveissière, 1973; Challier et al., 1977) was used to capture samples of tsetse. Tsetse were sampled for four to six consecutive days during the long, short and intermediate rains and also during the dry season. Twelve biconical traps were used and they were spaced at about 50 m intervals along thicket-grassland interfaces. Some 24-h samples were taken but whenever possible dissections were done in the field with cages being emptied every hour. This reduced mortality due to heat.

Identification of the trypanosomes was based on the location of the trypanosome in the tsetse (Lloyd and Johnson, 1924). The age of female tsetse was determined by examination of their ovaries (Saunders, 1962; Challier, 1965). The infection rate in animals was determined by taking two capillary tubes from each animal, centrifuging the blood and examining the buffy coat for trypanosomes. Thick and thin smears were also made.

Analysis

The simplest model of tsetse picking up an infection assumes that the survival rate of infected and uninfected flies is the same and that tsetse of all age categories have equal probability of picking up infection (Rogers and Boreham, 1973). These assumptions will be reviewed in the discussion but if valid then the probability of a fly remaining uninfected after k ovarian cycles (P_0) may be estimated using the binomial theorem:

$$P_0 = q^k$$

where

q = the probability of a fly not being infected during one ovarian cycle

p = the probability of a fly being infected during one cycle and thus $p + q = 1$

Hence $\ln(\text{proportion of flies uninfected}) = \ln q \cdot k$

A plot of the natural log of the proportion of flies uninfected against age group (k) should give a linear relationship with slope (b) of $\ln q$. Then $p = 1 - e^b$

If *G. pallidipes* take an average of 3.5 blood meals per ovarian age category (Snow and Tarimo, 1983), then the probability of the fly picking up an infection per blood meal (p') is

$$p' = 1 - e^{-\frac{b}{3.5}}$$

A similar approach was used by Rogers and Boreham (1973).

Results

The number of flies dissected in each age group for each locality and the incidence of infections are shown in Table 1. If the assumptions required in the analysis are met, the relationship between infection rate and ovarian age category should be curvilinear since infection rises asymptotically to a theoretical maximum of 100% with age. Results from all areas were pooled for each of the three trypanosome species and plotted against estimated age in days (Fig. 1). For both *T. vivax* and *T. congolense*, a curvilinear relationship of the form $Y = aX^b$ provided the best fit to the data (although it should be noted that the significance levels cannot be regarded as fully reliable since age cannot be measured without error). There was no such relationship for *T. brucei* (Table 2).

\ln (proportion of uninfected flies) was plotted against ovarian age category for each locality for *T. vivax* and *T. congolense*. Comparison of the slopes showed that results for Shimba Hills and Mwalewa could be pooled as could those for Muhaka and Ukunda. Results for Diani have been analysed separately (Fig. 2). Regressions were all significant with the exception of *T. congolense* in Diani (Table 3).

The probability of a single blood meal giving rise to an infection was then calculated (Table 3). Whilst the probabilities of acquiring *T. congolense* and *T. vivax* infections were similar in Shimba Hills/Mwalewa, that for *T. congolense* was much greater than *T. vivax* in two areas where domestic animals were common (Ukunda/Muhaka). In Diani, however, the data suggested a lower probability of acquiring *T. congolense* than *T. vivax*.

Host infection rates were only determined at Diani (Table 4). The average host interaction rate was 10.3% whilst the overall probability of a tsetse developing an infection after a single blood meal was 0.0034 in Diani. This would mean that only 3.3% of the infected blood meals eventually give rise to an infection in the fly. Given the likely underestimate of suid infection rate, this percentage (3.3) should probably be even lower. This demonstrates the existence of a substantial barrier to infection (Rogers, 1979b).

Discussion

Ryan et al. (1982) plotted infection rate versus age of the tsetse and obtained linear relationship. Although this is an adequate empirical procedure

Table 1. Infection rate of *Trypanosoma congolense*; *T. vivax* and *T. brucei* in relation to age of *G. pallidipes* in Ukunda, Diani, Muhaka, Shimba Hills, and Mwalewa

Study area	Tssetse age groups (days)							Total	
	Ovarian age category		10-19		20-29		30-39		
	0-9	10-19	20-29	30-39	40-49	50-59	60-69	70-79	
Ukunda	No. dissected	35	39	62	44	72	64	53	43
	<i>congolense</i>	0	0	5	12	13	13	8	412
	<i>vivax</i>	0	0	0	0	0	1	0	51
	<i>brucei</i>	0	0	0	0	0	0	0	1
Diani	No. dissected	271	609	522	404	368	208	182	2680
	<i>congolense</i>	3	22	20	29	20	8	13	5
	<i>vivax</i>	2	9	13	6	16	12	9	120
	<i>brucei</i>	0	0	0	0	0	1	0	73
Muhaka	No. dissected	162	300	255	204	241	160	132	1548
	<i>congolense</i>	2	5	15	18	29	17	20	118
	<i>vivax</i>	0	4	4	5	3	4	6	29
	<i>brucei</i>	0	0	0	0	0	0	0	0
Shimba Hills	No. dissected	182	604	590	402	387	251	178	2722
	<i>congolense</i>	3	15	21	15	21	11	5	99
	<i>vivax</i>	1	19	9	20	18	13	17	106
	<i>brucei</i>	0	2	1	1	1	1	1	8
Mwalewa	No. dissected	191	501	389	289	304	214	157	2154
	<i>congolense</i>	2	13	14	7	18	15	12	86
	<i>vivax</i>	2	14	7	8	5	11	8	60
	<i>brucei</i>	0	1	0	1	1	0	0	5

* one *brucei* observed in another experiment not included

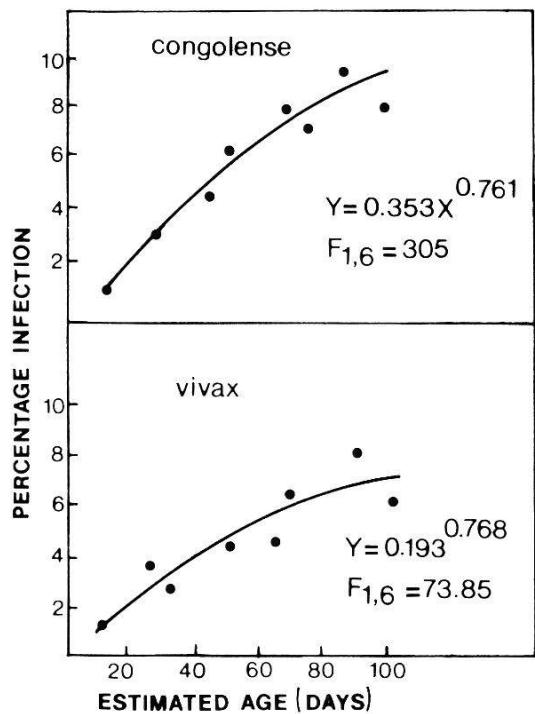


Fig. 1. Pooled results for percentage infection rates by two trypanosome species plotted against estimated age of female *G. pallidipes*.

Table 2. *T. brucei* infection in *G. pallidipes* at Shimba Hills and Mwalewa, in relation to the age of the tsetse

	Age groups							Total		
	0a	0b	1	2	3	4	5			
No. dissected	373		1105	979	691	3431	465	335	237	4876
% positive	0		0.36	0.20	0.15	0.06	0.04	0.30	0.42	0.27

when infection rates are low, it cannot explain the process of acquiring infection. Since infection rate in the flies increases with age, there is an increasing probability of already infected flies becoming reinfected, resulting in a simple curvilinear relationship. Moreover there is evidence that only a portion of the tsetse population is susceptible to trypanosomes (Maudlin, 1982), which would accentuate curvilinear relationship.

The major problem with all data relating infection rate to ovarian age, however, is the grouping together of tsetse age groups. Age categories 4–7 include ages 8–11, 12–15, etc. Since these very old flies (which are more likely to be infected) are included they tend to increase the infection rates in categories 4–7. The same technique was, however, employed in all the localities and therefore comparable estimates of rate of acquiring infection among the localities were obtained.

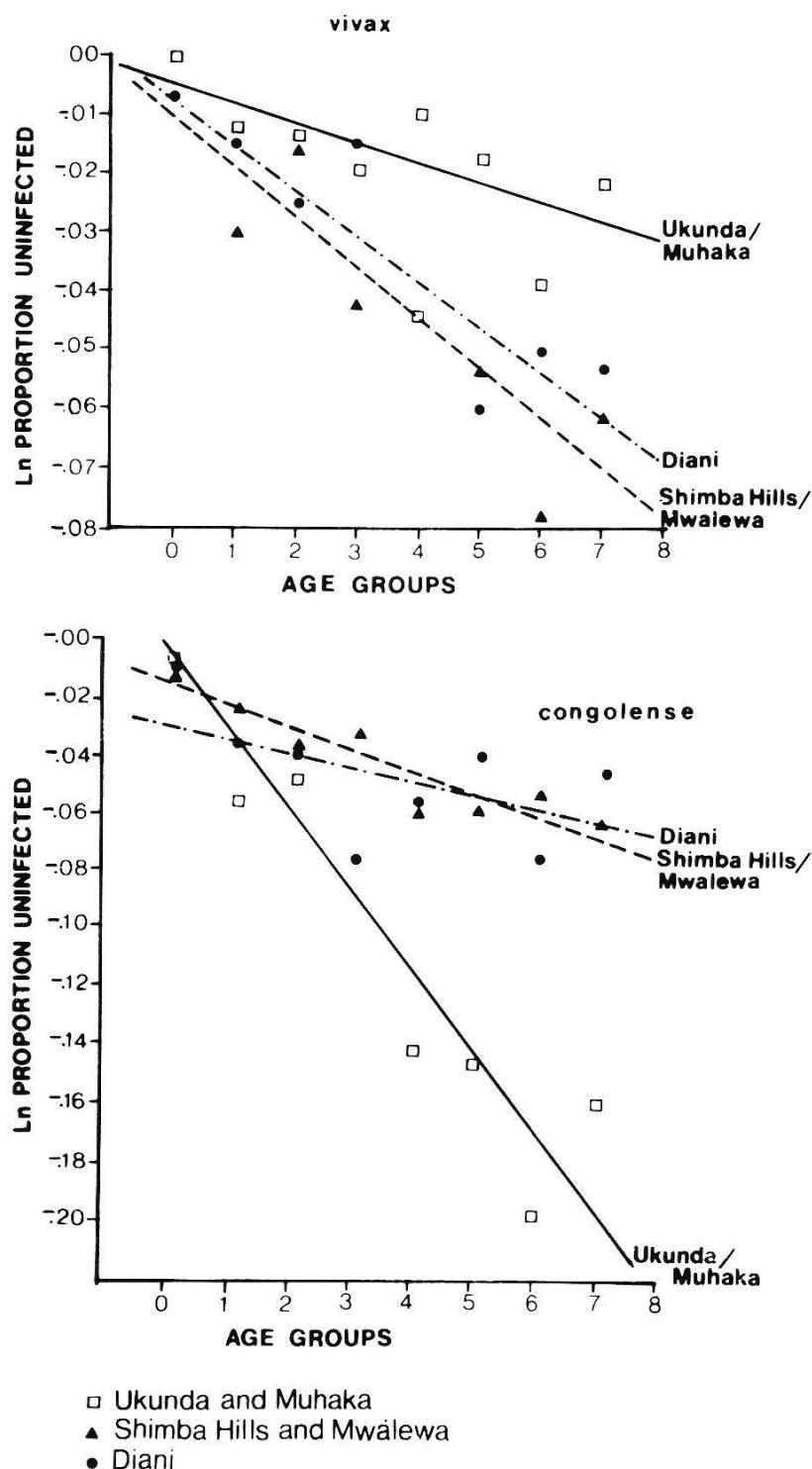


Fig. 2. \ln (proportion of uninfected *Glossina pallidipes*) plotted against ovarian age for the study localities for *Trypanosoma vivax* and *T. congolense* (the equations for the slopes are in Table 2).

In the present study, the probability of acquisition of trypanosomes by tsetse of different ages was assumed to be constant. However, this may not be the case. Although too few *T. brucei* were collected in the present study for any conclusive evidence, there was an indication that the rate of acquisition of *T. brucei* was not constant, and that *G. pallidipes* picks up *T. brucei* infections

Table 3. Regression details and calculation of the probabilities of single blood meals of *G. pallidipes* being infected in Ukunda/Muhaka, Shimba Hills/Mwalewa and Diani

Locality	<i>T. congolense</i> Regression equation	r	F 1,6	<i>T. vivax</i>		r	F 1,6	Λ p'		Total Λ p'
				Λ	p'			Λ	p'	
Ukunda and Muhaka	$Y = -0.0065 - 0.0270X$	-0.948	53.55***	0.0077		$Y = -0.0045 - 0.0035X$	-0.757	8.06*	-0.0010	0.0087
Shimba Hills and Mwalewa . . .	$Y = -0.0118 - 0.0068X$	-0.916	31.31**	0.0019		$Y = -0.0105 - 0.0085X$	-0.894	23.99**	-0.0024	0.0043
Diani	$Y = -0.0303 - 0.0047X$	-0.548	2.57 ns	0.0013		$Y = -0.0073 - 0.0075X$	-0.900	25.67**	0.0021	0.0034

$Y = \ln$ proportion uninfected

$X =$ Ovarian age

$r =$ Correlation coefficient

$F =$ F test for r

$\Lambda_{p'} =$ Estimated probability of a tsetse picking an infection in one blood meal
* $0.01 < P < 0.05$ ** $0.001 < P < 0.01$ *** $P < 0.0001$

Table 4. Feeding preferences of *G. pallidipes* and host infection rates at Diani, Kenya

Tsetse feeds (%)	Number of animals examined	Percentage of trypanosome infection in these animals	Average infection rates weighed by % feeds
Cattle/calves	38	34.2	
Goats/sheep	86	11.6	10.3
Suids*	4	0.0	

* Since only 4 suids were examined, the percentage trypanosome infection rate is clearly underestimated

only early in life. Wijers (1958) observed that the chances of a tsetse becoming infected with *T. brucei* increased if the first blood meal taken was infected. Gingrich et al. (1982), however, reported that starving four-day-old tsetse before feeding them can significantly increase their chances of becoming infected with *T. brucei*.

Whether the survival rate of infected flies is the same as that of uninfected or not (as assumed in the present study) has been a controversial issue. Jenni et al. (1980) reported that the feeding behaviour of infected tsetse differed from that of uninfected control flies and suggested that differences in feeding behaviour resulted from impaired function of the labral mechanoreceptors in infected tsetse. Roberts (1981) observed that infected tsetse probed more often than uninfected ones. Golder et al. (1982) put forward a hypothesis based on these experiments that infected flies are less healthy than uninfected ones which was supported by his observation that infected insecticide treated flies have a higher mortality than uninfected ones. Moloo (1982), however, differed from the above workers and maintained that there was no significant difference in feeding behaviour between infected and uninfected tsetse. These two opposing views need to be resolved as soon as possible as this would have a bearing on the estimate of trypanosome challenge, and the epidemiology of trypanosomiasis.

In Serengeti, Rogers and Boreham (1973) found that for *G. swynnertoni* the probability of acquiring infection for *T. vivax* varied from 0.026–0.0027 while for *T. congolense* it was 0.0027. These figures are of the same order of magnitude as for *G. pallidipes* in the present study (a computational error in the original analysis gave figures for these probabilities three times higher than they should have been (Townsend and Rogers, pers. comm.).

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