Observations on the behavior of Tsetse flies (Glossina morsitans orientalis Vanderplank and G.pallidipes Austen) during an attempt to concentrate breeding around cattle

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OBSERVATIONS ON THE BEHAVIOUR OF TSETSE FLIES
(GLOSSINA MORSITANS ORIENTALIS VANDERPLANK
AND G. PALLIDIPES AUSTEN) DURING AN ATTEMPT
TO CONCENTRATE BREEDING AROUND CATTLE

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Initial investigations into the sterile male technique as a means of eradicating Glossina morsitans (Knipping 1963; Simpson 1958) have been described by Dame, Dean & Ford (1964). This method of control requires large numbers of male flies for treatment and subsequent release into the natural population. Numerous attempts to breed tsetse flies under laboratory conditions have almost always failed because of poor survival or reproduction (Buxton 1955), but more recently Nash, Jordan & Boyle (1966) with G. austeni and Azevedo & Pinhao (1964) with G. morsitans have reported considerable success. Current investigations into the sterile-male technique included studies into the breeding of tsetse flies under field conditions. This paper presents results obtained from an attempt to concentrate breeding of a natural fly population based on the assumption that G. morsitans and G. pallidipes would aggregate around cattle permanently held in the bush. The availability of flies in different vegetation communities were assessed also in order to confirm the choice of habitat used for this study. This work was done in the Zambezi Valley, Rhodesia during 1965-67.

LIFE CYCLE AND ENVIRONMENT

Tsetse flies feed exclusively on vertebrate blood (Buxton 1955; Glasgow 1963). The female fly is larviparous, generally producing a single larva about every 10–14 days which enters the soil and pupates. The puparia of Glossina morsitans and G. pallidipes appear to be concentrated into certain definite sites at different periods during the year (Jackson & Phelps 1967). At the beginning of the dry season puparia are commonly found in the sand of dry river beds, under leaves and in the soil under fallen logs. During the hot months at the end of the dry season they are concentrated almost entirely into ant-bear holes, while their distribution appears to be more widespread during the rains between November and April. The pupal stage lasts for 28 days at 25°C, and the male and female flies become sexually mature within 7 and 3 days, respectively, after eclosion (Dame & Dean, unpublished).

The Zambezi Valley is a wide, generally flat, tree-covered plain lying at about 1300 ft above sea level and bordered by steep escarpments. The experimental area lay about 2 miles from the river and 8 miles east of Chirundu (15°55′ S, 29°10′ E). Small rivers in the area acted as temporary drainage lines and carried water only after rain. In this study four main types of vegetation community were recognized, but some species were common to all communities. The trees were in leaf during the rainy season and were generally bare, except for scattered 'evergreens', during the dry months.

Riverine-mopane community

This community is formed by a belt (50–100 yd wide) of dense, relatively low shrubs, containing a variety of tall trees, along the river bank, and flanked on either side by

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Breeding behaviour of tsetse flies

extensive stands of tall mopane (Colophospermum mopane). High and dense grass species flourish along the river bank during the wet season. The dominant top storey species of tree are *C. mopane* (50 ft), *Acacia tortilis* (50 ft), *A. nigrescens* (40 ft), *Kirkia acuminata* (55 ft) and *Tamarindus indica* (50 ft). The under storey contains mainly *Combretum molle* (25 ft), *C. mossambicense* (10 ft), *Psorolaelia obovata* (15 ft), *Dalbergia melanoxylon* (10 ft) and *Dichrostachys glomerata* (15 ft).

Mopane community

This community covers flat and gently rolling terrain with a low and sparse grass cover. It is open and dominated by an upper storey of *Colophospermum mopane*, *Kirkia acuminata*, *Lonchocarpus capassa* (40 ft) and scattered *Acacia nigrescens* (30 ft). Occasional clumps of shrubs contain *Pterocarpus rotundifolius* (15 ft) and *Combretum molle*.

Combretum community

This site was situated in relatively hilly country with poor grass cover. *C. molle* (15 ft) is the dominant shrub, under a relatively scattered upper storey of *Colophospermum*, *Kirkia acuminata* and *Euphorbia ingens* (25 ft).

Commiphora–mopane community

The rolling terrain is covered by dense bush, numerous trees of medium height, and has a poor grass cover. *Commiphora sp.*, *Kirkia acuminata*, *Colophospermum mopane* and *Acacia tortilis* (45 ft) form the upper storey. The lower bush contains mainly *A. ataxacantha* (20 ft) with *Combretum mucronatum*, * Diospyros quedoensis* (3 ft), *Ostryoderris stuhlmannii* (20 ft) and *Erythroxylum manii* (15 ft).

Large game animals were not commonly observed in these communities during the experimental period of 26 months. However, sightings and inspection of spoor indicated that impala, wart-hog, bush-pig and duiker commonly, and kudu, rhinoceros and elephant occasionally, occurred in, or passed through, the area.

METHODS

This study incorporated two related but separated trials. The first trial was started in January 1965 and lasted until February 1966. Three experimental areas were sited in the riverine-mopane community along the Mwangu River (Fig. 1 A–C). Cattle stockades and huts for the herders and stores were built by site C and in the centre of the grid at B, and a water pipe was laid to each point from the main camp supply 3 miles away. Shelters with thatched roofs and no walls were built at all proposed catching points to shield the oxen from direct sunlight.

The tsetse fly populations in the three areas were sampled twice a week. The initial phase of the first trial lasted from January into February 1965, when three oxen were taken to each site on the day of sampling only, and were not left there permanently. Flies landing on one out of the three oxen tethered within 30 yd of each other were caught between 05.00 and 18.30 hours. Each fly was marked before release with coloured oil paint by the 25 000 system (Jackson 1953) to ensure that the same fly was not recaptured and recorded twice on the same day. The second phase in the trial lasted for a further month and three oxen were tethered every day at points B and C, while oxen were taken to the control point A only for the bi-weekly sampling. Finally, eight oxen were
tethered individually 400 yd apart to form a grid around the original group of three oxen at point B. All the oxen at B and C were kept at night in the stockade and they were moved to and from their individual stations along certain definite paths so as to have least effect on the vegetation.

The second trial was begun during August 1965 along the Mwangu river and about a mile south of the cattle grid used in the first trial (Fig. 1 D). A weekly survey of the tsetse fly population was started by again catching flies off one out of three oxen tethered within 30 yd of each other. A 5-ac paddock was built next to this catching point, and huts for

![Diagram of research area at Chirundu](image)

**Fig. 1.** The research area at Chirundu. A, The location of the control point; B, cattle grid; C, site with three permanent oxen; D, 5 ac paddock; E, sample sites in mopane; F, *Combretum*; G, *Commiphora*-mopane. Fly-rounds 1-5 are also indicated.

herdsmen and stores were sited a ½ mile away from the paddock so that any effect of human habitation on the fly population might be minimized. The paddock was stocked with fifteen cows and oxen in January 1966, and the trial continued until February 1967. Sampling was done at weekly intervals, and the control point (A) with no animals permanently tethered there was retained as a control.

The fly densities in adjacent mopane (E), *Combretum* (F) and *Commiphora*-mopane (G) communities (Fig. 1) were similarly surveyed at weekly intervals throughout 1966 as
Breeding behaviour of tsetse flies

additional controls, and to confirm that the riverine-mopane was the most favourable habitat for the main trials. A full range of seasonal larviposition sites occurred around and within the grid and paddock areas.

Records were kept for every sampling period and site between 05.00 and 18.30 hours. The species and sex of each fly caught was recorded for each half-hour period, but no differentiation was made between gorged and non-feeding flies. Air temperatures and relative humidities were measured with a whirling hygrometer every half-hour.

The cattle used in these trials were exposed to infection by trypanosomes and were maintained successfully under a regular drug routine. Samorin (isometamidium) was injected subcutaneously into both sides of the neck every 2 months at a dosage level of 0.5 mg/kg body weight in a 0.5% aqueous solution, or 4.5 ml/100 lb body weight. This was a relatively low dose level and every second treatment was followed a week later by an injection of 3.5 mg of Berenil (diminazine aceturate)/kg body weight in a 7% solution, or 3.5 ml/100 lb body weight, to kill any trypanosomes that might have escaped the Samorin treatment. Blood smears taken from every animal 1 week before each treatment did not reveal any parasites during the trials. Stomoxys calcitrans (Diptera) and ticks worried the animals during the wet season without causing any serious health problems. These pests were not controlled chemically except for a short period during November and December 1965 when 5% BHC was used.

RESULTS

Patterns of diurnal activity

The total numbers of male and female Glossina morsitans and G. pallidipes caught at half-hour intervals in the riverine-mopane community between January and December 1966, and the corresponding mean half-hourly temperatures and relative humidities (05.00–18.30 hours), are given in Figs. 2 and 3. Data obtained from the other three communities were found to be similar and are omitted. Activity of G. morsitans was fairly evenly distributed throughout the day (06.00–18.30 hours) between January and April, though fewer flies were caught in the middle of the day than at other times. Temperatures were low from May to August and activity began later in the day (06.30–08.00 hours), ended earlier (18.00 hours), and reached a peak after midday. During the hot months of September to November-December flies were caught from first light (05.00 hours) and up to dusk (18.30 hours). The distribution of catches formed morning and afternoon peaks and few flies were caught during the hottest hours when temperatures approached and exceeded 30° C. Activity increased in the afternoon during October when temperatures were falling but were still above 30° C.

G. pallidipes were caught primarily in the afternoon between January and August, and the first captures were made later in the day than with G. morsitans (Fig. 3). Larger numbers were caught in the morning from August to December, but the afternoon peak remained dominant except in October. The times of first and last captures during these hot months were similar to those for G. morsitans.

Start of activity related to climate

The relationship between first capture and prevailing climatic conditions showed a difference between the two species of tsetse fly (Fig. 4). During the hotter months, January–April and September–December, the temperature at first capture of G. morsitans decreased and increased directly with the minimum daily temperature. There was no
Fig. 2. Total numbers of male (closed columns) and female (open columns) Glossina morsitans caught off oxen at half-hour intervals between 05.00 and 18.30 hours in riverine mopane.
Breeding behaviour of tsetse flies

Fig. 3. Total numbers of male (closed columns) and female (open columns) *Glossina pallidipes* caught off oxen at half-hour intervals between 05.00 and 18.30 hours in riverine-mopane. Mean air temperatures (°) and relative humidities (%) are shown.
correlation between May and August when minimum temperatures ranged from 9 to 16° C and first captures were made between 13 and 14° C. These temperatures at first capture were lower than those recorded by Jack (1939) and Pilson & Pilson (1967).

The first G. pallidipes were caught later in the day than G. morsitans, except between September and December, and at temperatures above the 13–14° C apparently restricting the activity of G. morsitans. Temperatures at first flight appeared to be directly related to minimum daily temperature. However, the pattern formed a cycle through the year compared with the more linear relationship shown by G. morsitans. The relatively small population of G. pallidipes from January to July may have biased the results for this species, and, a linear relationship between activity and climate may occur in all months. The relationship between temperature at first flight and maximum daily temperature was erratic for both species of tsetse fly.

![Climatographs showing relationship between climatic conditions at first capture of Glossina morsitans (---) and G. pallidipes (-----) and mean minimum and maximum daily temperature and mean daily humidity (05.30-18.30 hours) between 1 January and 12 December 1966.](image)

The relative humidity at first capture of G. morsitans increased and decreased directly with mean daily humidity (05.30–18.30 hours) throughout the year. The relationship between the humidity at the first appearance of G. pallidipes and mean daily humidity was very erratic. This may have been due to the large variations in the time of day and temperature when this species became active.

**Availability of tsetse flies in different vegetation communities**

The mean daily catch of tsetse flies in four different communities relatively close together is shown in Fig. 5. Only small numbers of either species were caught between January and July, but the daily catches were generally similar between successive samples within site, and between the different communities. Larger numbers of flies were caught as temperatures increased from August onwards, and this was followed by a decrease in numbers between October and November to a low level by December–January.
Breeding behaviour of tsetse flies

All the data obtained from weekly sampling in the riverine-mopane community during September–November 1966 are combined in Table 1. The daily catch for both species of

![Graph](image)

**Fig. 5.** Mean and range of daily catch of (a) *Glossina morsitans* and (b) *G. pallidipes* in four vegetation communities. ●, Riverine-Colophospermum; ■, Colophospermum; ▲, Commiphora; ◆, Combretum.

Table 1. Numbers of *Glossina morsitans* and *G. pallidipes* caught off bait oxen during weekly sampling in riverine-mopane between September and November and prevailing climatic conditions

<table>
<thead>
<tr>
<th>Week ending</th>
<th>Number caught</th>
<th>Mean maximum temperature (°C)</th>
<th>Mean humidity (%) (08.00 hours)</th>
<th>Total rainfall (mm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>September</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>112</td>
<td>31.6</td>
<td>57</td>
<td>0</td>
</tr>
<tr>
<td>14</td>
<td>190</td>
<td>36.6</td>
<td>55</td>
<td>0</td>
</tr>
<tr>
<td>21</td>
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<td>31.1</td>
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<td>28</td>
<td>152</td>
<td>40.0</td>
<td>45</td>
<td>1.8</td>
</tr>
<tr>
<td>October</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>184</td>
<td>38.9</td>
<td>46</td>
<td>0</td>
</tr>
<tr>
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<tr>
<td>19</td>
<td>167</td>
<td>38.3</td>
<td>49</td>
<td>0</td>
</tr>
<tr>
<td>26</td>
<td>187</td>
<td>37.7</td>
<td>35</td>
<td>0</td>
</tr>
<tr>
<td>November</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>72</td>
<td>41.1</td>
<td>22</td>
<td>0</td>
</tr>
<tr>
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<tr>
<td>16</td>
<td>93</td>
<td>39.4</td>
<td>52</td>
<td>68.0</td>
</tr>
<tr>
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<td>46</td>
<td>35.5</td>
<td>55</td>
<td>19.2</td>
</tr>
<tr>
<td>30</td>
<td>34</td>
<td>39.4</td>
<td>42</td>
<td>0</td>
</tr>
</tbody>
</table>

tsetse fly declined after 26 October. This decrease began after 5 weeks with maximum temperatures generally exceeding 38°C (100°F), with many days above 40°C. Relative
humidities were low during this period and the fall in the numbers of flies caught began before the start of the rains. Observations by Jack & Williams (1937) suggest that the cause of this decline in numbers may be due to starvation since the high temperatures inhibit activity and the ability to search for food during all but a small part of the day.

The data show that *G. morsitans* was fairly evenly distributed throughout all vegetation types during most of the year and tended to become more abundant in mopane and riverine-mopane communities, than in *Combretum* and *Commiphora*-mopane, only during September and October (Fig. 5a). From August to November, *G. pallidipes* was generally captured in larger numbers in the riverine-mopane than in adjacent stands of the other communities (Fig. 5b). In this respect, there seemed to be some difference in the distribution of the two species, but there were large ranges in the daily catch and it was impossible to determine whether the difference was significant. The populations in all four habitats increased during August and September. However, a decline in the numbers of both species in *Combretum* and *Commiphora*-mopane started between September and October while a decrease occurred only between October and November in the other two communities.

**Proportion of male and female flies**

The capture data show that more male than female *G. morsitans* were caught, while generally female *G. pallidipes* were more abundant than the male flies (Fig. 6a and b). Elosion of flies from 'wild' puparia held in the laboratory during the same period showed that male and female flies appeared in almost equal numbers (Dean, Wilson & Wortham 1968). Considerable variations in the percentage of female flies in the daily catch occurred between January and August, and no community appeared to consistently contain more of one sex than another. During the hot dry months, when more
Breeding behaviour of tsetse flies

flies were caught, the percentage of females in the daily catch became more constant, and the mean sex ratio for all habitats combined approached 1:1 more closely than during the rest of the year. Female flies of both species appeared to be more abundant in the riverine-mopane than in the other communities between August and October.

Tsetse fly populations around cattle in the riverine-mopane community

Trial 1. The mean and range of daily catch of the two species of tsetse fly during trial 1 are shown in Fig. 7. Low and similar numbers of G. morsitans were caught at the three sites (cf. Fig. 1) during January and February 1965, and similar numbers of G. pallidipes were obtained up to June. The presence of three oxen stationed permanently at one site, which was abandoned in October, and the eleven oxen in the grid did not produce an aggregate of flies around them. Between March and November larger numbers of G. morsitans were caught at the control point where there were no cattle stationed permanently. There was little difference in the mean number of G. pallidipes caught at the three sites.

Trial 2. Sampling at the paddock and control sites during trial 2 showed similar fly densities between August 1965 and June-July 1966. Cattle were put into the paddock during January 1966. Mean daily catches indicated that there were larger numbers of flies of both species around the paddock from about July to December-January. However, the ranges of daily catch were large and there was probably no significant difference in the populations with or without a permanent food supply.

The two trials lasted for a combined period of 26 months and the results showed seasonal variations in the numbers of both tsetse fly species. G. morsitans started to increase in March 1965, but did not do so until after June in 1966; while G. pallidipes became more numerous from August onwards in both years. Peak numbers generally occurred during the hot dry months and minima during the rainy season. This seasonal cycle in the apparent size of the fly populations occurred in both years, in all vegetation communities (Fig. 5), and independently of the absence or presence of cattle. Thus, a permanent food supply did not modify those factors, probably climatic, influencing the natural increase and decrease of the fly population.

DISCUSSION

The patterns of diurnal activity of Glossina morsitans co. form closely to those obtained by Pilson & Pilson (1967) at a higher altitude (3240 ft) and in rather different vegetation types. Activity by G. pallidipes resembled that of G. morsitans, and the pattern observed by Vanderplank (1948) and Leggate & Pilson (1961); only during the hot months from September to December. During the rest of the year the activity of this species began late in the day and occurred mainly in the afternoon. Vanderplank detected a difference in the diurnal rhythm of male and female G. palpalis but no such difference was detected in the present studies with G. morsitans and G. pallidipes.

Prevailing climatic conditions apparently affect the activity of both species. Tsetse flies seem to become conditioned to the prevailing temperature regime and, above 16–18° C, temperature at first capture seems to be related directly to the minimum daily temperature. The data show a relationship between humidity at first capture and mean daily humidity in G. morsitans but not in G. pallidipes. Maximum daily temperatures did not appear to influence the start of activity.

Lewis & Taylor (1963) showed that light intensity affected the flight activity of many
Fig. 7. Mean and range of daily catch of *Glossina morsitans* and *G. pallidipes* and prevailing climatic conditions during trials 1 and 2. ●, Control point; ▲, three oxen; ■, grid of twelve oxen; □, paddock with fifteen oxen.
Breeding behaviour of tsetse flies

insects; while Barrass (1962) found that activity of \textit{G. pallidipes} was inhibited by periods of high light intensity at temperatures below $32^\circ$ C. Vanderplank (1948) reported a negative correlation between light intensity and the number of \textit{G. pallidipes} caught at different times of the day. Pilson & Pilson (1967) suggested that the absence of morning peaks of activity with \textit{G. morsitans} during the wet and cool seasons might be a combined effect of light and temperature; when the threshold of $18^\circ$ C was reached, the light intensity was high enough to inhibit flight. This factor may be even more pronounced with \textit{G. pallidipes}, and would explain the dominance of the afternoon peak between January and August. Temperatures above $30^\circ$ C and high light intensities were possibly responsible for reducing activity during the middle of the day between September and November (Pilson & Pilson 1967). The importance of light was indicated further by the almost complete absence of \textit{G. morsitans} from before dawn and after dusk. Buxton (1955) indicates that some, though perhaps limited, activity may occur when it is dark if the temperature is high enough, but it is possible that such activity was due to disturbance by the observer. However, Chorley & Hopkins (1942) considered that \textit{G. pallidipes} can be active during moonlight nights.

It would appear that a wide range of communities in the Zambezi Valley are inhabited by \textit{G. morsitans} and \textit{G. pallidipes} at all seasons. This conclusion generally agrees with the results obtained by Pilson & Pilson (1967), except that they found male \textit{G. morsitans} concentrating into riverine vegetation during the hot months. The results given above, obtained from a different area and altitude, do not show an aggregation of males into this community at any time of the year; while female flies tend to become somewhat more available in all communities during the hot months.

Pilson & Pilson (1967) reported that in twenty-one out of thirty-two of their observations on gorged \textit{G. morsitans} caught off an ox there was no significant deviation from a 1:1 sex ratio. Lloyd (1912) also noted that gorged male and female flies were caught in almost equal numbers. However, Buxton's summary of results obtained by other workers using a variety of methods showed that the proportion of females caught is usually much less than 50%. He indicated also that the percentage of female \textit{G. pallidipes} in the catch was often lower than in the present studies, but Leggate & Pilson (1961) caught an excess of female \textit{G. pallidipes} over male flies.

Pilson & Harley (1959) reported that \textit{G. morsitans} in Uganda could maintain themselves on cattle and there were similar unpublished reports in Rhodesia during 1965. Glasgow (1961) found that tsetse flies were distributed in a negative binomial fashion (Bliss & Fisher 1953) and he detected 'concentration areas' which seemed to follow, and be caused by, the larger game animals. Nash (1933) produced an artificial concentration of \textit{G. morsitans} in relatively open country by making paths up to a waterhole that was not being used by game at that time. Similar paths were made to and from the centre of the cattle grid in trial 1 of these current studies. Jackson (1955) concluded that movements by herds of game, such as buffalo, were unlikely to cause mass displacements of flies, and large game animals were uncommon in the experimental areas during 1965–67. This suggests that tsetse flies in an area containing a low game population might be attracted to, and be aggregated around, cattle maintained in the riverine-mopane community. However, this study, involving both a grid of tethered oxen and a paddock containing free-roaming animals, showed that the presence of a permanent food supply does not necessarily produce a concentration of tsetse flies. Jackson (1955) found a negative correlation between numbers of flies and numbers of ungulates, and a positive correlation between the numbers of ungulates and the hunger of flies. This agrees with a
feeding ground theory that hungry flies move to a food supply but do not stay by it after feeding (Buxton 1955). Inspection of data of recaptured, marked flies showed that flies marked at the grid or paddock could be caught at any of the other points, or along fly round transects (Fig. 1) covering a much larger area of the surrounding bush (Dean, unpublished). It is possible that a changing adult population masked an increase in the puparial population within the experimental areas. However, this is unlikely since there was not an increase in the number of teneral flies caught off the bait oxen.

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SUMMARY

Investigations into diurnal activity and seasonal distribution of Glossina morsitans and G. pallidipes, with or without the presence of cattle as a permanent food supply, were carried out in the Zambezi Valley, Rhodesia during 1965–67. Tsetse flies landing on one of three oxen tethered close together were caught, marked and released. Records of captures and meteorological conditions were kept for each half-hour period between 05.00 and 18.30 hours. Results from weekly sampling in four different vegetation communities indicated that flies were evenly distributed throughout the bush between January and August, while riverine-mopane generally contained larger numbers of both species during the hot dry months. More male than female G. morsitans were caught off the oxen, but female G. pallidipes were more abundant than the males. The sex ratio of both species emerging from pupae was near equality. No other difference between the vegetation communities could be detected except that there appeared to be a higher percentage of female flies in the riverine-mopane than in the other communities during August–October.

G. morsitans was not active below 13–14°C and G. pallidipes below 16°C, and first captures of both species appeared to be conditioned to prevailing minimum daily temperatures. Activity was not detected before dawn or after dusk. The pattern of diurnal activity varied from season to season, and between the two species except from September to November.

Trials involving a grid of eleven tethered oxen, and a 5-ac paddock containing a herd of fifteen animals, showed that a permanent food supply neither concentrated tsetse flies, nor influenced seasonal fluctuations in the numbers.

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Breeding behaviour of tsetse flies


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