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Productivity of *Glossina morsitans morsitans* Westwood maintained in the laboratory, with particular reference to the sterile-insect release method

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Glossina morsitans *is of great economic importance in Africa and if a mass-rearing project were to be undertaken with a view to control by the release of sterilized males it would be necessary to know the productivity that could be obtained from this species in the laboratory. Data for life tables and age-specific fecundity schedules of* G. m. morsitans *fed on goats or lop-eared rabbits are used to calculate outputs of viable pupae or of young adult males that would be available for disposal.*

For control by the sterile-male method, it is likely that pupae bred in captivity would be the organisms of choice for field release. The weekly output of viable males could be 18–25 % of the total adult stock. Some implications of these findings are discussed.

Procedures for rearing tsetse flies at this laboratory were developed with *Glossina austeni* Newst. and a self-maintaining and productive colony of this species has been in existence since 1966 (Nash, Jordan & Boyle, 1968). Jordan & Curtis (1968) and Curtis & Jordan (1970) calculated the productivity that could be obtained from *G. austeni* under the maintenance conditions at this laboratory, when fed on either goats or lop-eared rabbits.

In early 1967, a colony of *G. morsitans morsitans* Westwood [2] was established with pupae from Kariba, Southern Rhodesia. Satisfactory rearing techniques for *G. austeni* had taken some three years to develop (Nash, Jordan & Boyle, 1968) but, employing the same techniques, the *G. morsitans* colony immediately became self-maintaining. Since the performance of *G. morsitans* under laboratory conditions shows some differences from that of *G. austeni*, and owing to the importance of *G. morsitans* as the principal vector of animal trypanosomiasis and as a vector of sleeping sickness in some areas, it seemed desirable to repeat the productivity calculations for this species. Such information would be helpful if mass-rearing of *G. morsitans* were to be undertaken in Africa with a view to control by the sterile-male method. *G. austeni* is a relatively unimportant species and advanced methods of control involving mass rearing would probably be unjustified.

As in the previous papers (Jordan & Curtis, 1968; Curtis & Jordan, 1970) a distinction is made between colonies in the " expanding phase " and the " stationary phase ". In the expanding phase all offspring produced by the colony are retained in the colony and growth is exponential; r_m, the innate capacity for increase in numbers (Andrewartha & Birch, 1954), gives a measure of the rate of growth of such a colony.[3] The stationary phase of a colony is that which occurs when it is maintained at a constant size and all surplus offspring are removed from the colony for some purpose such as sterilization and release; performance in this phase can be measured in terms of its output of disposable offspring.

Both goats and lop-eared rabbits are used as hosts for *G. morsitans*, and the productivity of the latter when fed on each host is described.

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[2] *Glossina morsitans orientalis* Vanderplank is a synonym of this species (Machado, 1970).

[3] r_m is related to the growth of an expanding colony as follows:

$$N_t = Noe^{r_m t}$$

where t is a time interval in days and N_o and N_t are the number of females in the colony at times o and t.

METHODS

Experimental procedures

The fly room is maintained at about 25°C and at a relative humidity of 60–70%.

The data employed are from life-tables and age-specific fecundity schedules constructed from the emergence rate from pupae and the subsequent longevity and fecundity of females.

Emergence rates from pupae are based on 45 392 pupae deposited as larvae by females kept in cages stored on an aluminium rack (Nash, Jordan & Trewern, 1971). The pupae were collected daily and stored until emergence in large cages, in artificial light; the effective emergence rate was 96.4%.

Females were mated when they were 3 days old, with males at least 15 days old. The data for females until the end of the 24-h mating period are taken from 1 242 females fed daily on goats since emergence and from 1 220 fed on rabbits; 95.3% of the former and 96.5% of the latter were alive at the end of this period.

The data for the post-mating life of females are from an experiment in which 210 females were kept 15 per cage and fed on rabbits' ears and a second experiment in which 500 were kept 25 per cage in larger cages and fed on goats. The flies fed on rabbits produced in their lifetime a mean of 10.3 pupae per mated female; the comparable figure for those fed on goats was 7.4. The overall productivity of these flies was comparable with that of other contemporary groups of females fed on the two hosts (Nash, Jordan & Trewern, 1971).[1]

Calculation procedures

The method of calculating r_m is that of Birch (1948); the details of the method as applied to tsetse populations are given by Jordan & Curtis (1968). The female life-table begins at the time of deposition as a larva and is divided into 9-day time units or age groups. The first five time units are passed in pre-reproductive stages and it is not until the sixth that the first larva is produced. Thereafter one larva could be produced in each time unit.

The age-specific fecundity of females in each time unit is the number of female pupae produced divided by the number of females surviving. In *G. morsitans* the number of female pupae is half the total number of pupae. Production of a larva from each ovulation by all females surviving would result in a constant value of 0.5 for age-specific fecundity.

The number of offspring that can be disposed of from a colony in the stationary phase is arrived at by the method of Monro & Osborne (1967), as modified for tsetse populations by Curtis & Jordan (1970). In the case of *G. austeni* it was found that each male was capable of inseminating six females and that it was necessary to keep each male for approximately four time units, after which they could be killed off. Recent work has shown that the same is true for *G. morsitans*. Thus the data and assumptions about the requirements for " stud " males in a breeding colony of *G. morsitans* are the same as those given by Jordan & Curtis (1968) for *G. austeni*.

RESULTS

The life tables for female *G. morsitans* when fed on either goats or rabbits are shown graphically in Fig. 1. Survival of the rabbit-fed flies was better than that of the goat-fed flies. The flies showed a marked aging effect, as can be seen by the fact that the time taken for successive halvings of the proportion surviving became progressively less. Both groups of flies showed this aging effect, although it became more pronounced earlier with the goat-fed females.

Age-specific fecundity of the females is shown in Fig. 2. With both groups of flies, fecundity remained at a high level until the flies were about 110 days old (corresponding to about 75 days of adult life) and then declined until the death of the last flies. There was no pronounced difference between the fecundity of flies fed on the two hosts.

From the data in Fig. 1 and 2 various alternative parameters that describe the performance of colonies in the expanding phase have been calculated and are given in Table 1.

For the stationary phase it is assumed that the surviving females are killed at the age that gives the

Table 1. Alternative measures of the maximum rate of increase of expanding colonies of *G. morsitans*

Method of raising *G. morsitans*	r_m	Doubling time	Increase in 1 year
goat-fed	0.0145	47.8 days	199-fold
rabbit-fed	0.0166	41.7 days	428-fold

[1] *Note added in proof (January 1972)*: The longevity of the females subsequently declined and this resulted in a reduced lifetime pupal production. The reason for the decline is not known.

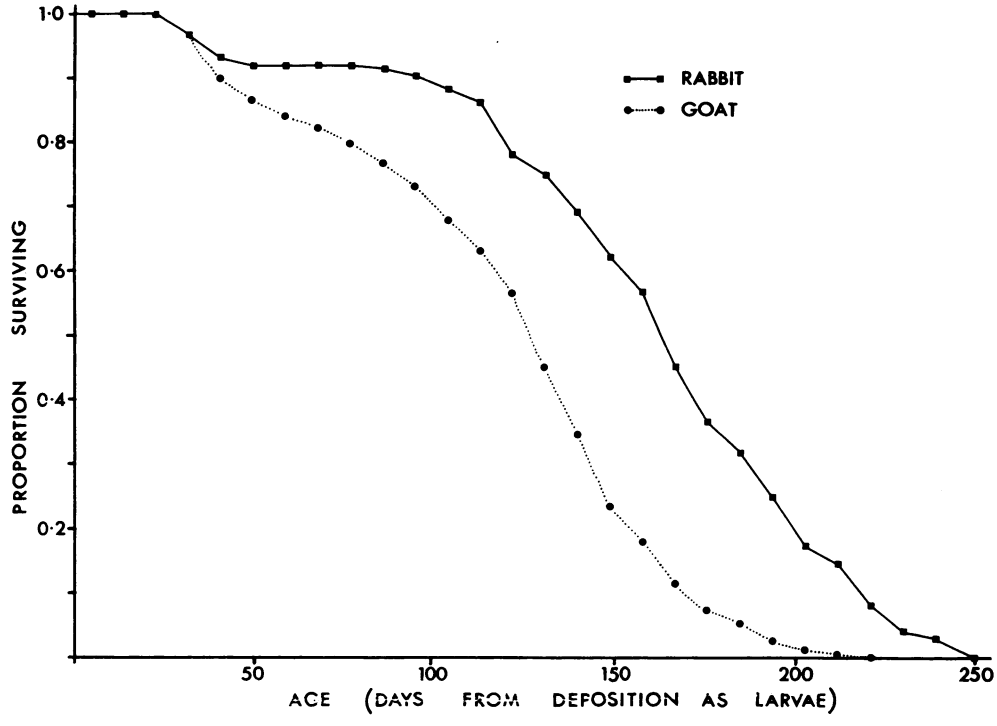

Fig. 1. Survival of goat-fed and rabbit-fed female *G. morsitans*.

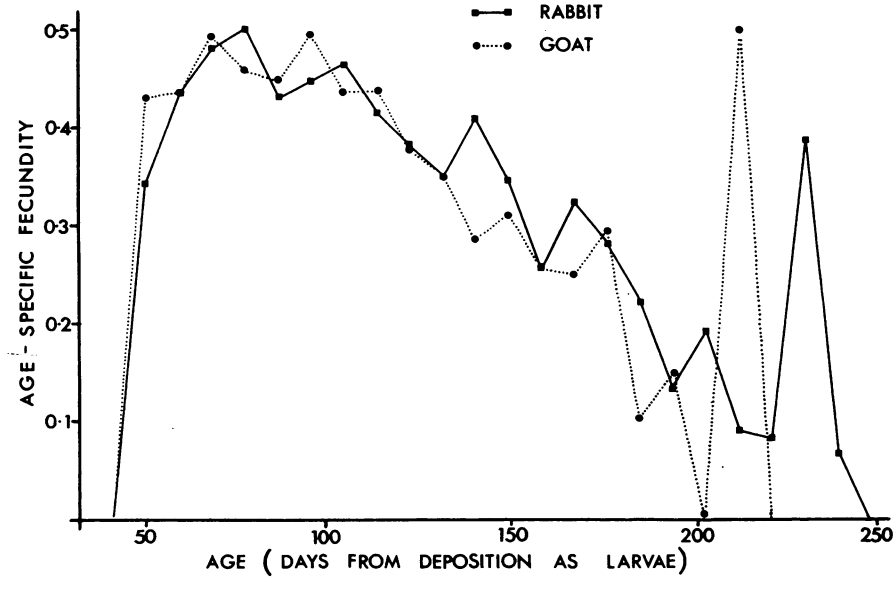

Fig. 2. Age-specific fecundity of goat-fed and rabbit-fed female *G. morsitans* based on the number of female pupae produced per surviving female in successive 9-day time units. No significance is attached to the fluctuations after about day 200 when there were very few surviving females.

Table 2. Estimates of weekly inputs and outputs for stationary colonies of 1 000 adult *G. morsitans*

Method of raising *G. morsitans*	Total production of viable pupae of each sex (1)	Input of viable pupae required to maintain colony		Disposable output in the form of	
		Female (2)	Male (3)	Viable pupae of each sex (4)	Young adult males (5)
goat-fed	257	76	13	181	244
rabbit-fed	259	56	9	203	250

optimum rate of output from the colony. If such females are retained beyond that age it would result in slightly reduced output from the colony because of the poorer fecundity of older females. Using the method of Curtis & Jordan (1970) it can be shown that surviving female *G. morsitans* (both those fed on goats and those fed on rabbits) should be killed at about 175 days of age, corresponding to an adult age of about 140 days.

Data for the stationary phase are given in Table 2. Column 1 shows the total weekly production, obtainable from colonies of 1 000 adult flies, of viable pupae of each sex (i.e., the total number of pupae produced multiplied by the observed rate of emergence). Columns 2 and 3 show the necessary input of females and males required to replace deaths in the breeding colony; the requirement for males is relatively low because, as noted above, each one can be used for six inseminations. Subtraction of column 2 from column 1 yields column 4, which is the disposable output of viable pupae of each sex. Since fewer males than females are required for return to the breeding colony, extra output of males is possible if the individuals disposed of are sexed. This maximum output of males is indicated in column 5, which is obtained by subtracting column 3 from column 1.

DISCUSSION

Under conditions at this laboratory, *G. morsitans* is a less productive species than *G. austeni*; this is also so at Maisons-Alfort, Paris (Itard & Maillot, 1970). Comparison of the data given in this paper with those for *G. austeni* (Curtis & Jordan, 1970) shows that *G. morsitans* is the shorter-lived species irrespective of whether goats or rabbits are the host. Whereas the life tables of *G. austeni* were similar for the two hosts, *G. morsitans* fed on goats survived less well than when fed on rabbits. Goat-fed *G. austeni* survived better than goat-fed *G. morsitans*, but, when rabbits were the hosts, the survival of *G. morsitans* was better than that of *G. austeni* until about 160 days of age (corresponding to about 125 days of adult life), although after that age *G. morsitans* aged and died more rapidly.

The reproductive life of *G. austeni* was longer than that of *G. morsitans* and age-specific fecundity began to decline at a much earlier age in the latter species. The age-specific fecundity of rabbit-fed flies was similar in the early age groups of the two species but with goat-fed flies it was actually higher in the first 8 productive age groups of *G. morsitans* than in *G. austeni*. Thereafter the age-specific fecundity of *G. morsitans* sharply declined, while it remained relatively high in *G. austeni* for about another 3 months.

As shown in Fig. 1 and 2, *G. morsitans* fed on rabbits had better survival but equal fecundity, compared with the same species fed on goats. Since fecundity alone determines the total rate of production from a given adult colony, the rate is very similar on the two hosts (Table 2). However, the poorer survival of goat-fed females means that more of the production would have to be retained to replace deaths in the breeding colony. If releases were made with unsexed pupae the disposable output of both sexes would therefore be about 11% less with goats than with rabbits. If all males were released, apart from the few needed as replacements in the breeding colony, the disposable output would be higher and very similar using either host (Table 2). To obtain this extra contribution to the output of males, separation of the sexes would be necessary, and this might be done at the adult stage. However, it appears that release before emergence of the adult is necessary to ensure the normal development of thoracic musculature (Dame, Birkenmeyer & Bursell, 1969). A system of releasing sterilized male pupae,

largely separated from females, has been proposed by Curtis & Langley (1971), based on the earlier hatching time of female pupae. If this proves to be practicable it would appear to make possible the rates of release of sterile males indicated in column 5 of Table 2.

It can be concluded that the weekly output of sterile males could be 18–25% of the total stock of adult flies (i.e., females and sufficient males for breeding purposes), depending on the host used and the form in which releases were made. In practice somewhat lower levels of disposable output than these would have to be accepted as it would be necessary to retain rather more pupae than the absolute minimum required to maintain the colony at constant size. A safety margin of pupae should always be retained to correct for periods of increased mortality, which occur even in the best managed colonies; there is always a risk of contamination of the colony with, for example, low levels of insecticide (Nash, Jordan & Trewern, 1971).

When deciding which host to use in a large-scale rearing project in Africa, the relatively small difference in fly productivity when fed on goats or rabbits would probably be less important than other factors, such as relative efficiency of fly feeding operations, host maintenance costs, and the resistance of each host to disease. The use of two unrelated host species would provide a safeguard against an epidemic.

It would be unrealistic to base the cost of a large-scale rearing project for *G. morsitans* in Africa on a scaling-up of the costs of production at a laboratory in Europe. Both capital and running costs would be different under African conditions. It can, however, be predicted that the mass rearing of tsetse for a sterile-male project will never be as cheap as is that of oviparous insect species. Because of the viviparity of the genus it will probably never be possible to increase the productivity of *G. morsitans* much above the values given in this paper. However, although the low reproduction rate of *Glossina* makes laboratory rearing difficult, a downward trend in its numbers in nature could probably be achieved with much lower ratios of sterile to fertile individuals, compared with those necessary for control of more rapidly reproducing insects.

It might be argued that laboratory rearing is not the most convenient method of producing large numbers of pupae for sterilization and subsequent release. It could be cheaper to collect pupae in the field, but this has the disadvantage that whereas in many areas it is possible to collect enormous numbers of pupae in the dry months of the year, few, if any, can be found during wet months. In addition to their availability throughout the year, laboratory-reared pupae have the major advantage that they are of known age. In order to obtain maximum sterility, with unimpaired viability of the sterilized adults, it is desirable that pupae of known age should be sterilized, regardless of the method of sterilization (see, for example, Dame & Schmidt, 1970).

The degree of success of a large-scale laboratory-rearing programme for *G. morsitans* in Africa would not depend entirely on the productivity of the colony. It would be necessary for the laboratory-reared insects to be comparable with native insects. It seems that this objective can be achieved as the *G. morsitans* produced at this laboratory, with mean weights of pupae of 29.6 mg and 30.7 mg, for flies fed on goats and rabbits, respectively (Nash, Jordan & Trewern, 1971), are equivalent in weight to wild pupae collected in Southern Rhodesia at different seasons (mean weight 30.0 mg—D. A. Dame, personal communication). It has also been found that *G. morsitans* reared at this laboratory, when released into the field in Southern Rhodesia as pupae, survived and dispersed as well as native flies (Dame & Schmidt, 1970). The available evidence suggests, therefore, that productive colonies of *G. morsitans* can produce insects that are fully comparable with wild tsetse, although their relative ability to find mates and to inseminate them in the field has not so far been determined.

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RÉSUMÉ

RENDEMENT DE *GLOSSINA MORSITANS MORSITANS* WESTWOOD ÉLEVÉE AU LABORATOIRE, CONSIDÉRÉ NOTAMMENT SOUS L'ANGLE DE LA MÉTHODE DU LÂCHER D'INSECTES STÉRILES

Grâce à l'établissement de tables de mortalité et à la détermination du taux de fécondité selon l'âge, on peut mesurer le rendement de lots de *Glossina morsitans morsitans* élevées au laboratoire sur des chèvres ou des lapins. Le facteur r_m (capacité naturelle d'accroissement d'une colonie) se situe à 0,0145 pour les colonies en expansion nourries sur chèvres et à 0,0166 pour celles qui sont maintenues sur lapins, le temps nécessaire au doublement de la population étant de 47,8 jours dans le premier cas et de 41,7 jours dans le second. En se basant sur le rendement d'une colonie stationnaire (dont la population est maintenue à un niveau constant par retrait de la descendance en excès), on estime que la production hebdomadaire de mâles pourrait être de l'ordre de 18 à 25 % de la population adulte totale de la colonie.

On s'accorde à penser que pour lutter contre *G. morsitans* par la méthode des mâles stériles, le mieux est de libérer les insectes dans la nature sous forme de nymphes. Il semble possible de différencier partiellement les sexes d'après le temps nécessaire à l'éclosion imaginale, et d'arriver ainsi à lâcher un maximum d'insectes mâles en retenant les quelques spécimens nécessaires à la reproduction ou destinés à pallier une éventuelle surmortalité au sein de la colonie.

Le rendement des colonies de *G. austeni* est supérieur à celui des élevages de *G. morsitans*, dont la durée de vie en captivité et de fécondité est moindre. Pour les deux espèces, et surtout pour *G. austeni*, la production est plus élevée lorsque les insectes sont nourris sur le lapin.

Il semble que les colonies de *G. morsitans* élevées au laboratoire puissent engendrer des nymphes de poids comparable à celui des nymphes issues de glossines sauvages et également aptes à donner des adultes capables de se disperser et de survivre dans la nature.

REFERENCES

Andrewartha, H. B. & Birch, L. C. (1954) *The distribution and abundance of animals*, University of Chicago Press, Chicago, Ill., USA

Birch, L. C. (1948) *J. anim. Ecol.*, **17**, 15-26

Curtis, C. F. & Jordan, A. M. (1970) *Bull. ent. Res.*, **59**, 651-658

Curtis, C. F. & Langley, P. A. (1971) *Trans. roy. Soc. trop. Med. Hyg.*, **65**, 230

Dame, D. A., Birkenmeyer, D. R. & Bursell, E. (1969) *Bull. ent. Res.*, **59**, 345-350

Dame, D. A. & Schmidt, C. H. (1970) *Bull. ent. Soc. Amer.*, **16**, 24-30

Itard, J. & Maillot, L. (1970) *Les élevages de glossines à Maisons-Alfort (France)*. In: *Proceedings of the First International Symposium on Tsetse Fly Breeding Under Laboratory Conditions, Lisbon, 1969*, pp. 125-136

Jordan, A. M. & Curtis, C. F. (1968) *Bull. ent. Res.*, **58**, 399-410

Machado, A. de B. (1970) *Les races géographiques de* Glossina morsitans. In: *Proceedings of the First International Symposium on Tsetse Fly Breeding Under Laboratory Conditions, Lisbon, 1969*, pp. 471-486

Monro, J. & Osborn, A. W. (1967) *Aust. J. Zool.*, **15**, 461-473

Nash, T. A. M., Jordan, A. M. & Boyle, J. A. (1968) *Ann. trop. Med. Parasit.*, **62**, 336-341

Nash, T. A. M., Jordan, A. M. & Trewern, M. A. (1971) *Mass rearing of tsetse flies* (Glossina *spp.*): *recent advances*. In: *Proceedings of the IAEA/FAO Symposium on the Sterility Principle for Insect Control or Eradication, Athens, 1970*, pp. 99-110