Ann. Soc. belge Méd. trop.
1985, **65**, 191-197

METHODS TO CALCULATE SURVIVAL RATE IN TSETSE FLY (*GLOSSINA*) POPULATIONS

by

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Summary — A simple method of calculating the daily survival rate (or mortality) of a female tsetse population is described, based on the geometric mean survival per ovarian cycle of an age-graded sample and the duration of the interlarval period. The method was applied to samples from three tsetse species and compared with survivorship curve estimates. The validity of the method when applied to biased samples is discussed.

KEYWORDS : Tsetse Flies; *Glossina palpalis*; *G. pallidipes*; Survival Rate; Populations.

Introduction

Forces act on a population determining its distribution and abundance. Survival rate is a measure of the strength of these forces and is therefore an important parameter in population dynamics studies. For disease transmitting organisms, population density and longevity are amongst the factors determining vectorial capacity; survival rate is thus important also in the epidemiology of vector-borne diseases. Saunders (9) devised a method by which a female tsetse population survivorship curve could be obtained from the probable age composition of a sample, using Challier's (1) improved version of Saunders' (7) original age categorisation by ovarian arrangement. Briefly, the cyclical development of tsetse ovarioles enables eight ovarian age categories to be recognised on dissection. The first four of these (designated 0, 1, 2 and 3) enable the fly to be aged accurately; the last four (4 + 4n, 5 + 4n, 6 + 4n and 7 + 4n) are composite categories, from which it is not possible to determine whether a fly is in its 4th, 8th, 12th...; 5th, 9th, 13th...; etc... ovarian cycle. Such is determined probabilistically from the sample as a whole, based on an assumed logarithmic death rate.

We proposed to show that Saunders' method can be refined further : by estimating a daily survival rate, and by simplifying the computational steps from which it is ultimately derived.

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Methods

Daily survival rate from the survivorship curve equation

The survivorship curve is commonly used in the form $\log y = a + bx$, where y is the number of females in each ovarian category x, a is the log of the number of flies on day 1, and b is the log of the survival rate per ovarian cycle. If the duration of each ovarian cycle is λ days, then the daily survival rate, Φ is given by $=$ antilog b/λ.

The duration of the ovarian cycle (= interlarval period) is temperature dependent, and reference is made to the formula in Glasgow (5) for calculating this when the temperature is known.

By way of an example, the probable age composition of a *Glossina palpalis gambiensis* Vanderplank sample from the Kou Forest, Upper Volta (2) was computed by Saunders' method and the equation $\log y = 2.54551 - .1192x$ for the survivorship curve was obtained. From mark/release/recapture data at the same time, the interlarval period was between 9 and 10 days. The daily survival rate was therefore between antilog $- .1192/9 = .970$, and antilog $- .1192/10 = .973$.

Simplified methods of calculating daily survival rate

Considering successive ovarian cycles of 4, the survival rate between ovarian categories 0 and $(4 + 4n)$ is given by the ratio $(4 + 4n)/(0 + (4 + 4n))$. This by log transformation becomes $\log (4 + 4n) - \log (0 + (4 + 4n))$. Similarly for the survival rates between categories 1 and $5 + 4n$, 2 and $6 + 4n$ and 3 and $7 + 4n$. This gives four equations (A, B, C, D) :

(A) $\log (4 + 4n) - \log (0 + (4 + 4n))$
(B) $\log (5 + 4n) - \log (1 + (5 + 4n))$
(C) $\log (6 + 4n) - \log (2 + (6 + 4n))$
(D) $\log (7 + 4n) - \log (3 + (7 + 4n))$

from which the mean log survival rate per four cycles is $[(A) + (B) + (C) + (D)]/4$, and the survival rate per cycle is antilog $[(A) + (B) + (C) + (D)]/16$. This simplifies to :

$$\Phi = \text{antilog} \left[[\log (4 + 4n) \ldots + \log (7 + 4n)] - [\log (0 + (4 + 4n)) \ldots + \log (3 + (7 + 4n))] / 16\lambda \right], \text{ (daily survival rate).}$$

The application of this geometric mean formula, using Challier's (2) data, is shown in Table 1. Transformations are based on log 10n to eliminate a negative index. For small samples, when zero values are likely to occur in some ovarian categories, the transformation $\log 10(N + 1)$ should be used.

A feature of Saunders' probabilistic method is that the bigger the sample size the greater the number of probable age categories it produces. This has the effect of slightly over-estimating the survival rate when the sample is large and vice-versa. This is illustrated also in Table 1, where

TABLE 1

Application of geometric mean method to calculate daily survival rate, from *Glossina palpalis gambiensis*

A. — Actual numbers of females from the field sample

Ovarian category	Number of females	Ovarian category	Number of females
0	48*	4 + 4 n	15
1	28	5 + 4 n	16
2	20	6 + 4 n	13
3	9	7 + 4 n	8

B. — Calculation of the daily survival rate

$\log (10 \times 15) = 2.1761$
$\log (10 \times 16) = 2.2041$
$\log (10 \times 13) = 2.1139$
$\log (10 \times 8) = 1.9031$
8.3972

$\log (10\,[48 + 15]) = 2.7993$
$\log (10\,[28 + 16]) = 2.6435$
$\log (10\,[20 + 13]) = 2.5185$
$\log (10\,[9 + 8]) = 2.2304$
10.1917

$$\text{Daily survival rate : } \phi = \text{antilog } \frac{8.3972 - 10.1917}{16\,\lambda\,^{**}}$$

$$= .972 \; (\lambda = 9)$$
$$= .975 \; (\lambda = 10)$$

C. — Daily survival rates from survivorship curve based on different numbers of ovarian categories

Number of ovarian categories	r^{2***}	Coefficient b	Survival rate (= 9)	(= 10)
20	.919	− .1098	.972	.975
16	.930	− .1111	.972	.975
12	.930	− .1151	.971	.974
8	.895	− .1299	.967	.971

* Non tenerals only.
** Interlarval period in days.
*** Coefficients of determination of survivorship curve equations, all highly significant (P .001) by t-test.

survival rates were calculated on the basis of 20, 16, 12 and 8 categories. Since only the 3rd decimal place of the survival rate is affected, it is not necessary to base calculations on more than 12 categories. Furthermore, it is unlikely that in nature females would survive beyond (13 × 10 =) 130 days.

There is no real necessity for using a geometric mean; an arithmetic mean should serve equally well, and this further simplifies calculations. This is illustrated below, using the same data as in Table 1.

$$\text{Arithmetic mean survival rate/ 4 cycles} = \left[\frac{15/63 + 16/44 + 13/33 + 8/17}{4}\right] = .36657.$$

$$\text{Daily survival rate} = \text{antilog} \left[\frac{\log .36657}{4\,\lambda}\right]$$

$$= .973 \; (\lambda = 9)$$
$$= .975 \; (\lambda = 10).$$

Sampling bias

For the estimated survival rate to be an accurate measure of the true rate the sample age composition must be representative of the population age structure. It is well known, however, that the age composition of a sample differs according to the sampling method and the species samples (8). Furthermore, teneral females, which form part of the nulliparous (O) ovarian age category, are most affected. For all species, these are generally over-estimated in hand-net capture samples, and it is commonly the practice to exclude them from age composition calculations. We propose to show that there is a further source of sampling bias, which in itself indicates that different age strata of the population are to be found in different parts of the tsetse habitat. Numbers of females may be in excess in a particular or several age groups in relation to sampling sites (vegetation cover); for example, old flies category in villages, young flies in gallery forests (3). Table 2 shows the age composition of *G. palpalis palpalis* (R.-D.) (3) and *G. pallidipes* Aust. (unpublished data) sampled with biconical traps (4) simultaneously in three different parts of the habitat of the same population of each species. Survival rates were calculated to show the effect of sampling bias on this parameter. These were derived from the survivorship curve, the geometric mean and the arithmetic mean, to demonstrate further that similar results are obtained. The small differences between survival rates from geometric and arithmetic means are because the former is always less than or equal to the latter.

It can be seen, for both species, that the percentage of O category females varied considerably with trapping site, being greatest where the vegetation was densest and vice-versa. This may also relate to the proximity of traps to the breeding sites of these species. Furthermore, O category *G. pallidipes* females were markedly under-represented in samples from all three trapping sites, whereas O category *G. palpalis* females appeared to be under-represented in the sample from the village compound only. Under-represented O categories result in over-estimated survival rates. The comparatively poorer coefficients of determination for the slopes of the survivorship curves for *G. pallidipes* reflect mainly the gross under-representation of O category females in biconical trap samples of this species.

Further regarding under (and over-) -represented O category females: it is reasonable to suppose that by omitting these from calculations, together with the concomitent (4 + 4n) values, more realistic survival rate estimations would be obtained. Thus, in Table 1 above, the totals under B become 6.22115 and 7.39242 respectively. The daily survival rate from the geometric mean formula then becomes :

$$\Phi = \text{antilog}\ (6.22115 - 7.39242/(12\lambda))$$
$$= .975\ (\lambda = 9);\ .978\ (\lambda = 10).$$

Similarly from the arithmetic mean :

$$(16/44 + 13/33 + 8/17)/3 = .40939$$
$$\Phi = .40939^{1/(4\lambda)}$$
$$= .975\ (\lambda = 9;\ .978\ (\lambda = 10).$$

TABLE 2

Ovarian age composition of *Glossina palpalis palpalis* and *G. pallidipes* samples in biconical traps sited in three different parts of a habitat of each species, showing the effect of sampling bias on survival rate determinations

Species and locality	Trapping site	Ovarian categories 0 (% 0)	1	2	3	4+	5+	6+	7+	Daily survival rates : from A	*	B	C	D	E
G. p. palpalis	gallery forest	39 (39.1)	16	11	9	5	4	2	1	.948	(.983)	.946	.947	.948	.949
Koudougou-Carrefour,	coffee plantation	50 (33.3)	19	13	17	16	15	11	9	.973	(.939)	.972	.973	.976	.976
Ivory Coast	village compound	23 (17.0)	25	17	8	20	15	16	11	.979	(.933)	.979	.980	.979	.980
G. pallidipes	dense thicket	22 (18.3)	37	11	11	15	11	8	5	.967	(.839)	.970	.971	.968	.969
Lambwe, Kenya	conifer plantation	35 (13.3)	60	43	20	43	26	22	14	.973	(.962)	.974	.975	.971	.971
	open woodland	3 (2.5)	27	24	6	18	24	9	9	.982	(.536)	.981	.984	.977	.978

A : survivorship curve; * : r^2, coefficient of determination for survivorship curve; B : geometric mean; C : arithmetic mean; D : geometric mean, after omitting values in ovarian categories 0 and 4 + 4 n; E : arithmetic mean, ditto.

Survival rates calculated on the basis of an interlarval periode of 9 days for both sepcies.

The survival rates calculated after omitting categories O and (4 + 4n) are also shown in Table 2. The figures still indicate, for both species, that different parts of the habitat harbour different age strata of the population, older females being more prevalent in open areas.

Discussion

The advantages of the methods described are firstly that daily survival rate is introduced as a more usefull concept than the survivorship curve to describe mortality in a population; secondly, calculations of survival rate are much simplified. The main qualification concerns survival rate estimation from ovarian age composition data in general, which bears on the usefulness of this parameter for measuring mortality change in a population. The underlaying assumptions are that the mortality rate in each age category is constant, and that the population is relatively stable. These conditions may not be met where large seasonal (climatic) differences occur. These probably produce a complex interaction of fluctuating numbers of births and deaths, through varying lengths of ovarian developmental duration, and disproportionate mortality in different age groups (6, 10). Clearly, age grouping data must be treated with caution, especially when attempting to estimate population change from calculations of intrinsic rate of increase (9). The data presented here on sampling bias further illustrates the problem of sample representation of population structure.

Acknowledgments — *This work was part of a ICIPE (International Centre of Insect Physiology and Ecology) tsetse ecological research programme funded by DITH (Dutch International Help). The senior author was seconded from O. R. S. T. O. M. (Office de la Recherche Scientifique et Technique Outre-Mer, now Institut Français de Recherche Scientifique pour le Développement en Coopération).*

Dr W. F. Snow and Dr R. D. Dransfield are thanked for their useful criticism of an earlier draft of this manuscript. Dr J. Dejardin and Dr G. Pichon (ORSTOM) are thanked for their friendly help in statistics and the calculator programme respectively.

Méthodes pour calculer le taux de survie des populations de Glossines (*Glossina*).

Résumé — Une méthode simple pour calculer le taux de survie quotidien (ou la mortalité) d'une population de femelles de glossines est décrite; elle est fondée sur la moyenne géométrique de la survie par cycle ovarien à partir des groupes d'âge physiologique d'échantillons et sur la durée de la période interlarvaire. La méthode a été appliquée à des échantillons de trois espèces de glossines et a été comparée à des estimations de la courbe de survie. La validité de la méthode est discutée dans le cas d'échantillons biaisés.

Methodes om de overleving van tseetseevliegen (*Glossina*) te berekenen.

Samenvatting — Een eenvoudige methode om het dagelijks overlevingscijfer van vrouwelijke tseetseevliegen te berekenen wordt beschreven. Ze is gebaseerd op het meetkundig gemiddelde van de overleving per ovaria cyclus van een monster met gekende leeftijd en op de lengte van de interlarvaire periode.

Received for publication on October 31, 1984.

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