Parous Rate as a Function of Basic Population Parameters of Mosquitoes

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Abstract: A mathematical formula was derived to describe the parous rate as a function of basic population parameters of mosquitoes. The formula includes 4 parameters, the daily survival rate of adults, the number of gonotrophic cycles per life time, the length of a gonotrophic cycle and the finite rate of population increase. Using the formula, some simulation studies were made to compare the sensitivity of the parous rate to these 4 parameters. The importance of the daily survival rate of adults and the length of a gonotrophic cycle depends largely on the finite rate of population increase. The parous rate is more sensitively influenced by these two parameters when populations are decreasing than when they are stable or increasing. The number of gonotrophic cycles per life time is effective only when it is smaller than 7, therefore, its importance seems to be negligible in most of mosquito species.

Key Words: Mathematical formula, Parous rate, Population parameters

INTRODUCTION

The parous rate is one of the useful parameters to describe mosquito populations, although some problems for practical use still exist (Ungureanu, 1974; Service, 1976). One of the important parameters estimated from the parous rate is a daily survival rate of adult mosquitoes. The relation between the parous rate and the daily survival rate was given by Davidson (1954). But the formula holds only when the population achieves a stationary age distribution, that is, stable in density and in age structure. Usually the underlying assumptions are not valid in field populations and some practical methods have been proposed to estimate the survival rate from the parous rate in natural mosquito populations (Garrett-Jones and Grab, 1964; Birley and Rajagopalan, 1981; Birley and Boorman, 1982; Mutero and Birley, 1989).

The parous rate relates not only to the daily survival rate of adults but also to the recruitment rate of adults, the adult longevity and the length of a gonotrophic cycle. Therefore, changes in the parous rate reflect many aspects of the population changes. Several workers used the parous rate to compare the age composition in different popula-

tions of the same species or in the same populations under different conditions (Aniedu *et al.*, 1989; Samarawickrema *et al.*, 1987).

In aedine mosquitoes, the relationship between adult body size and vector capability of female mosquitoes has been studied recently based on the daily survival rate of adults estimated from the parous rate (Haramis, 1983; Nasci, 1986 a, b; Walker *et al.*, 1987; Landry and DeFoliart, 1987; Landry *et al.*, 1988). Excepting the daily survival rate of adults, there are no theoretical works on the relationship between the parous rate and other population parameters, and for this reason, it is not easy to conclude which is the main factor of the observed changes in the parous rate. Here, we present a mathematical formula that describes the parous rate as a function of the basic population parameters, and based on the formula, simulation studies were made to compare the effects of changes in some population parameters on the parous rate.

MATHEMATICAL FORMULATION

Assuming that females just after emergence do not come to feed on blood but they come **b** days after emergence and thereafter, come to feed on blood **n**-1 times every **g** days, the number of gonotrophic cycles per life time becomes **n** (Table 1).

Consider the total number of feeding females at time **t**, then
$$N_{t,b} + N_{t,b+g} + N_{t,b+2g} + N_{t,b+(n-1)g},$$
where $N_{t,x}$ is the number of females in age **x** at time **t**. Assuming the constant daily survival rate, **p**, then
$$N_{t,x} = N_{t-x,o}p^x.$$
Therefore, the total number of feeding females becomes
$$N_{t-b,o}p^b + N_{t-(b+g),o}p^{(b+g)} + N_{t-(b+2g),o}p^{(b+2g)} + N_{t-\{b+(n-1)g\},o}p^{\{(b+(n-1)g\}}$$
$$= \sum_{x=0}^{n-1} N_{t-(b+gx),o}p^{(b+gx)}.$$
Assuming a constant finite rate of the population increase per day, **r**, then $N_{t,o}$ becomes
$$N_{t,o} = r^x N_{t-x,o},$$
then $\quad N_{t-x,o} = r^{-x}N_{t,o}.$

Therefore, the total number of feeding females becomes
$$\sum_{x=0}^{n-1} N_{t,o} \; r^{-(b+gx)}p^{(b+gx)}. \quad\text{..} \quad (1)$$

Table 1. List of population parameters and their notation used in the text

g: length of a gonotrophic cycle
p: daily survival rate of adults
n: number of gonotrophic cycles per life time
R: finite rate of population increase per gonotrophic cycle

Table 2. Parameter values used in the simulation studies

g: 3, 4, 5
p: 0.5, 0.6, 0.9, 0.8, 0.9
n: 1 to 10
R: 0.5, 1.0, 5.0

Now consider the total number of nulliparous females in the feeding population. As mentioned above, all adults take a blood meal on **b** days after emergence and every **g** days thereafter, so that all of the feeding females older than **b** days are parous. On the other hand, the total number of newly emerging females which come to feed on **b** days after emergence equals to the the total number of nulliparous females in the feeding population.

(Total number of nulliparous females)$= N_{t, b} = r^{-b} N_{t, o} p^b$.

From eq (1), the parous rate is defined as follows

$$\text{Parous Rate} = 1 - \frac{N_{t, b}}{\sum_{x=0}^{n-1} N_{t, o}\, r^{-(b+gx)} p^{(b+gx)}}$$

$$= 1 - N_{t, o}(p/r)^b / N_{t, o}(p/r)^b \sum_{x=0}^{n-1}(p/r)^{gx}.$$

Through some calculations, we get the following equation

$$\text{Parous Rate} = (p/r)^g \{(p/r)^{g(n-1)} - 1\} / \{(p/r)^{gn} - 1\}. \quad\text{....................} \quad (2)$$

Using the survival rate per gonotrophic cycle, **S** $(=p^g)$, and the finite rate of population increase per gonotrophic cycle, $\mathbf{R}(=r^g)$, eq (2) becomes

$$\text{Parous Rate} = (S/R \{(S/R)^{(n-1)} - 1\} \{(S/R)^n - 1\}. \quad\text{.....................} \quad (2')$$

When **n** is indefinite and if $\mathbf{S/R} < 1$ then

$$\text{Parous Rate} = S/R = p^g/R, \quad\text{...} \quad (3)$$

and also if the population is stable in size, $\mathbf{R} = 1$, then

$$\text{Parous Rate} = S = p^g.$$

This is the formula given by Davidson (1954) to calculate the daily survival rate of adults from the parous rate.

Here, we have defined the parous rate as the rate of parous females in the feeding population. It should be noted that the parous rate thus defined is different from the rate of parous females in a whole female population which includes females in feeding, resting and ovipositing stage.

Simulation Studies and the Results

The parous rates were calculated from eq (2) using the parameter values listed in Table 2 and the results are summarized in Fig. 1. The upper graphs in Fig. 1 show the relation of the parous rate to the number of gonotrophic cycles per life time, **n**. The five curves from the top to the bottom in each graph show the relationship when **p** = 0.9, 0.8, 0.7, 0.6, and 0.5 are assumed in the calculation, respectively. The effects of **n** on the parous rate is greater when the finite rate of increase per gonotrophic cycle, **R,** is smaller and the daily survival rate, **p,** is higher. But **n** is effective only when it is smaller than 7, and when **n** = 10 the parous rates are very close to the values calculated from eq (3) in most of the cases. This means that eq (3) is applicable when **n** is larger than 10.

Using the parous rates shown in the upper graphs, the daily survival rates were estimated by eq (3) and shown in the lower graphs in Fig. 1. As shown in the previous sec-

tion, eq (3) is valid when **n** is large enough. Therefore, when **n** is small there is a large discrepancy between the actual value of the daily survival rate assumed in the calculation and the estimated value derived from eq (3), but the discrepancy becomes small as **n** becomes large. Except the lower left graph (**R** = 0.5), the curves approach gradually to the actual values of the daily survival rate and when **n** = 10 the discrepancies are less than 0.001 in most of the cases. When the daily survival rate assumed in the calculation is less than 0.8, the curves approach the actual values very soon and the discrepancy less than 0.001 was achieved when **n** = 5. The 3 curves for **p** = 0.9, 0.8 and 0.7 in the lower left graph show large discrepancies even when n is large. This is because of the small value of the finite rate of increase per gonotrophic cycle, **R**, assumed in the simulation. The eq (3) is derived under the condition of large **n** and **S/R** < 1. **S** is always less then 1 so that when **R** is larger than 1, eq (2) is always valid if **n** is large enough. But in decreasing populations where **R** is less than 1, in some cases like the 3 curves in the lower left graph, the condition **S/R** < 1 is not valid especially when **S** is large and **R** is small. In these cases we can not use eq (3) to estimate the daily survival rate and eq (2) should be used. The number of gonotrophic cycles per life
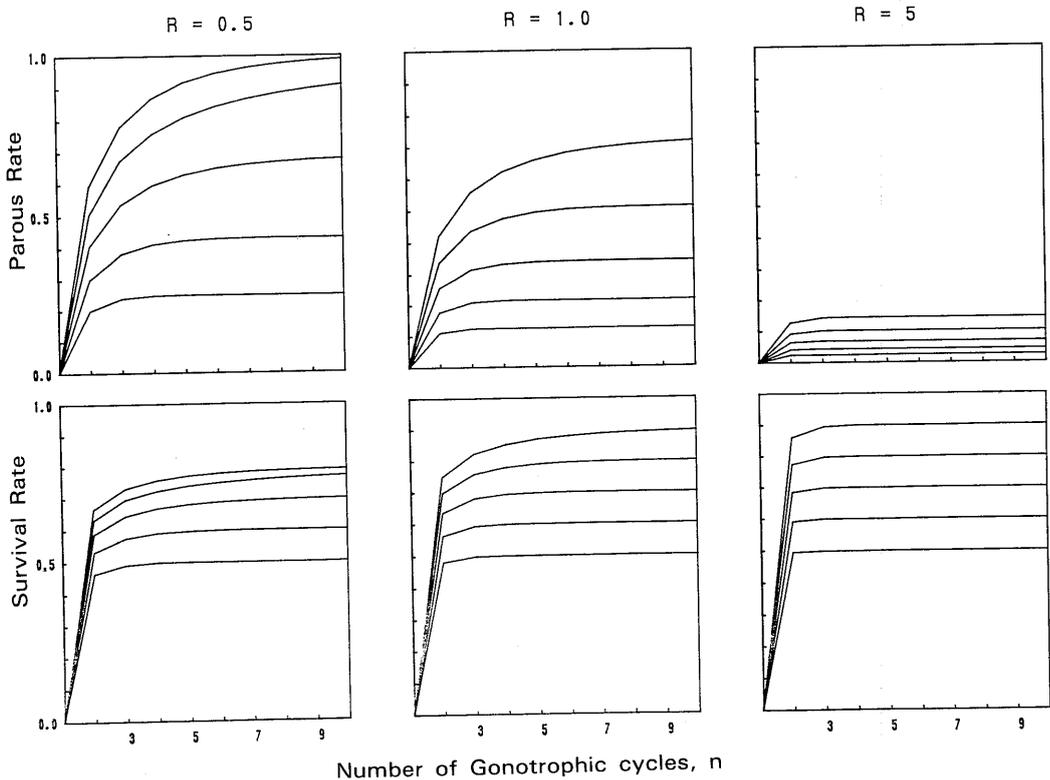

Fig. 1. The relationships of the parous rate to the number of gonotrophic cycles, **n,** (upper graphs) and the relationships of the estimated daily survival rate to **n** (lower graphs). Values of population parameters used in the simulation are listed in Table 2 (Here **g** is fixed to 3). Five curves from the top to the bottom in each graph show the relationship when **p** = 0.9, 0.8, 0.7, 0.6, and 0.5 were used in the calculation, respectively.

time, **n,** so far studied ranged from 4 to 12 (Chan, 1971; Charlwood and Wilkes, 1979; Detinova and Gillies, 1964; Gillies and Wilks, 1965; Kay, 1979; Samarawickrema, 1962, 1968; Samarawickrema *et al.,* 1987; Spencer, 1979) and most of mosquitoes of medical importance seem to have **n** around 10. Therefore, we can use eq (3) in most of the cases to estimate the daily survival rate of the adults when the populations are stable or increasing.

The effects of the finite rate of increase per gonotrophic cycle, **R,** on the parous rate were derived using eq (2') and shown in Fig. 2. The parous rate decreased as **R** becomes large, and rapid decrease occurs when **R** is around 1. Therefore, the finite rate of increase should be estimated very carefully even when mosquito populations are nearly stable in density. The daily survival rate of adults, **p,** also affects the parous rate greatly especially when the finite rate of population increase per gonotrophic cycle is between 0.2 and 2.0 (Figs. 1 and 2). In other words, the parous rate in decreasing populations depends largely on the daily survival rate of adults, **p.** In stable or increasing populations, the parous rate is more sensitive to the changes in **p** when the daily survival rate is large.

As to the length of a gonotrophic cycle, **g,** the larger **g** results in the lower level of the parous rate (Fig. 3). The importance of **g** largely depends on the finite rate of increase per gonotrophic cycle, **R,** and the parous rate changes greatly according to the increase of **g** value when **R** is less than 1. In conclusion, the importance of the length of a gonotrophic cycle, **g,** and the daily survival rate of adults, **p,** depends on the finite rate of population increase and the parous rate is more sensitive to **g** and **p** in decreasing populations than in increasing or stable populations. The number of gonotrophic cycles, **n,** seems to be large enough in most of the natural populations of mosquitoes, and for this reason the effects of **n** on the parous rate may be negligible.
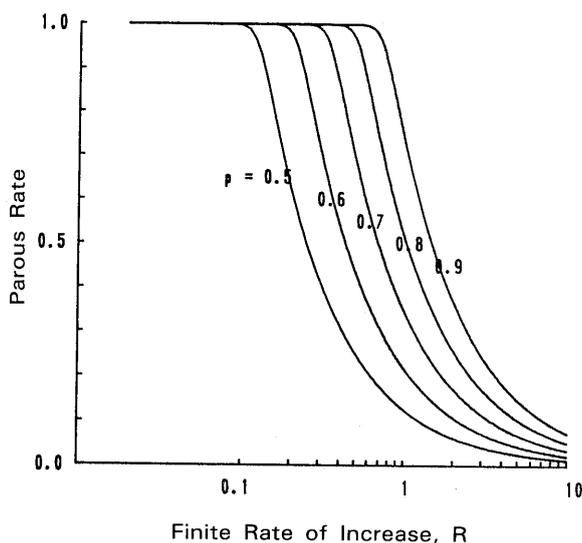

Fig. 2. The relationships of the parous rate to the finite rate of increase, **R,** for 5 different values of the daily survival rate, **p.** **g** and **n** were fixed to 3 and 20, respectively.

For the estimation of the daily survival rate of adults, eq (3) is applicable in stable or increasing populations. But in decreasing populations, where eq (3) is not always valid, it is better to use eq (2) instead of eq (3). The calculation of the daily survival rate of adults from eq (2) is not so easy that graphs shown in Fig. 4 would be helpful. Assuming $n = 10$ and $g = 3$, 4, and 5, the curves showing the relation between the parous rate and p are depicted for 14 different values of the finite rate of population increase (from 0.2 to 1.5). Using the figures we can find the daily survival rate from the observed parous rate as follows. If the observed parous rate is 0.6 and if we can suppose $g = 4$ days, and $R = 0.4$ then using the middle figure of Fig. 4 we can find the daily survival rate of around 0.7 in this case.
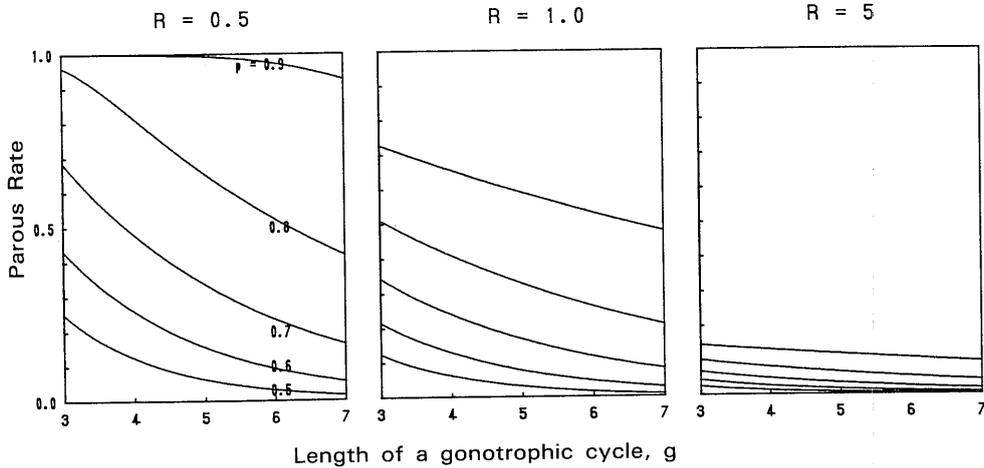

Fig. 3. The relationships of the parous rate to the length of gonotrophic cycles, g, for 3 different values of the finite rate of increase, R. The 5 curves in each graph show the relationship when 5 different values of the daily survival rate, p, were used in the simulation. n was fixed to 20.
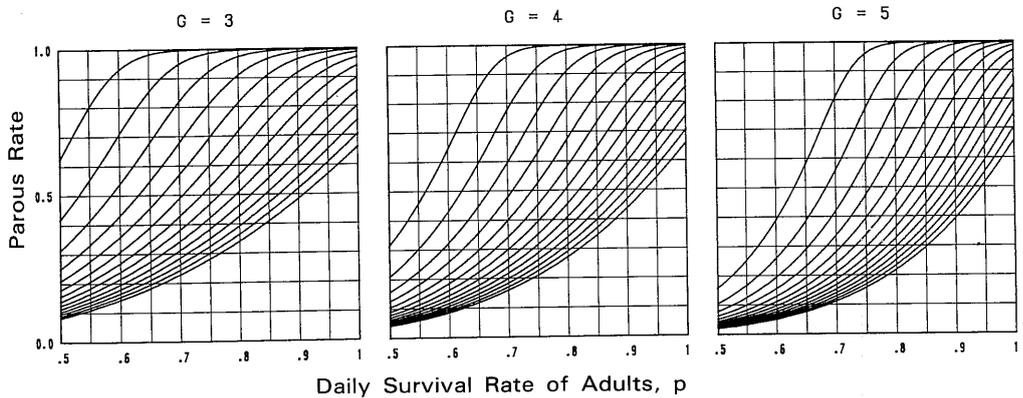

Fig. 4. The relationships of the parous rate to the daily survival rate of adults for 3 different values of g. The curves from the top to the bottom in each graph were derived assuming the 14 different values of the finite rate of increase, $R = 0.2$ to 1.5.

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