

Demography

**MATHEMATICAL DEMOGRAPHY OF *ODONTOTERMES REDEMANNI*
(WASMANN) (ISOPTERA : TERMITIDAE)**

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The intrinsic rate of increase or growth coefficient, r_m , of the mound-building termite *Odontotermes redemanni* (Wasmann) is estimated to be 0.96, giving a finite rate of increase of 0.007 individual per head per day. The net reproductive rate R_0 and gross reproductive rates are 10.02 and 19.17 respectively. The level of full utilization of growth potential depends on the functional needs of the colony. A review of the known examples from various groups of social insects shows that termites have the slowest rate of population production.

INTRODUCTION

In demography, intrinsic rate of increase, r_m , is a measure of success of a species under optimum physical and biological conditions (Andrewartha & Birch, 1954). Since it is greatly influenced by any subtle change in the environment or insect physiology (Fenchel, 1974), r_m has been mostly determined for laboratory populations (Banerjee, 1966 a; Birch 1948; Mertz, 1969), and rarely for field populations (Paris & Pitelka, 1962). The problems of its application to specific populations have been discussed by Jensen (1975).

The computation of demography for the social insects in general, and termites in particular, presents a series of statistical problems because most of these are difficult to rear in the laboratory ; this precludes direct estimation of some of the essential population parameters. Moreover, the caste system of termites, and the absence of a well marked female population which provides the basic data for constructing the fertility table, necessitate several theoretical assumptions and modifications of the conventional Leslie-Birch's method (Birch, 1948) in computing the intrinsic rate of increase and associated population parameters. This paper describes the basic demography for the mound-building termite, *Odontotermes redemanni* (Wasmann).

BASIC MODEL

The mathematics of population growth is that growth is exponential, at the rate r_m per individual, such that

$$dN/dt = r_m N, \quad \dots 1$$

where dN/dt is the rate of change in the population in a unit time t , N is the size of the population, and r_m is the intrinsic rate of increase of the population of a stable age distribution. On integration, Eq. 1 yields

$$N_t = N_0 e^{r_m t} \quad \dots 2$$

where N_t is the population at a time t , and N_0 — population on a previous occasion, and e is the base of natural logarithm.

The exponent coefficient of the population growth, i.e. the intrinsic rate of increase, r_m , is approximated by the Euler equation as

$$\int_0^{\alpha} e^{-r_m x} l(x)m(x)dx=1 \quad \dots 3$$

where $l(x)$ is the survival probability of the female at a particular age group (x), and $m(x)$ is the age-specific fecundity. Eq. 3 can be solved by iteration taking arbitrary values of r_m until the left hand side of equation is close to unity. Theoretically, a colony should maximize r_m to achieve a rapid growth.

COMPUTATION OF PARAMETERS

The statistical parameters needed for a numerical solution of Eq. 3 are x , $l(x)$ and $m(x)$. In computing these parameters for *O. redemanni*, several extrapolations and assumptions have been made.

Pivotal age (x)

Pivotal age used in the computation is the mid-point of age intervals. The females, i.e. the queens of *O. redemanni* are difficult to rear in the laboratory for a sufficiently long time to get a correct estimate of their ages. But the body measurements of a series of fecund females, starting from de-alate stage right up to physogastric stage, collected from mounds of known age, give an approximation of their age-structure.

A near linear relationship exists between the height and age of the mounds (Fig. 1) up to a height of 200 cm (log 2.31) when mounds are about four year old; after this the growth of the mounds levels off (Banerjee, 1975). Total body length of the queen, in turn, is positively correlated ($r = +0.89$, $P < 0.01$) with

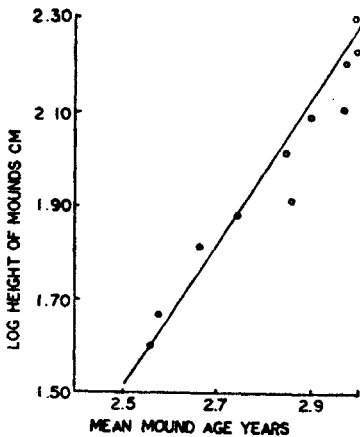


FIG. 1. Relationship between age and height of the mounds of *Odontotermes redemanni* (Wasmann).

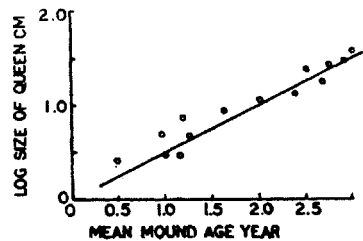


FIG. 2. Relationship between the body length of the queen and age of the mounds of *Odontotermes redemanni* (Wasmann).

the age of the mounds as reflected in their heights. Smaller mounds have smaller queens and the size increases with the age of the mounds (Fig 2).

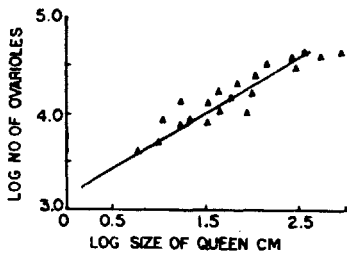


FIG. 3. Relationship between the no. of ovarioles and body length of the queens of *Odontotermes redemanni* (Wasmann).

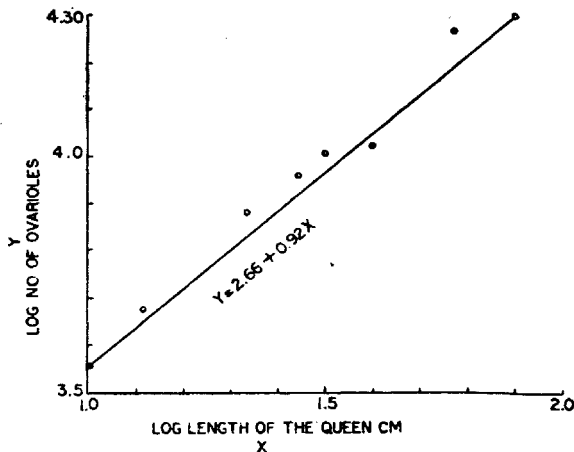


FIG. 4. Regression equation and fitted regression line to indicate the relationship between body length and number of ovarioles in the queens of *Odontotermes redemanni* (Wasmann).

Thus from the relationship, mound height : mound age : size of the queen, a good approximation of the pivotal age, classes of the queens, i.e. the females, can be obtained (Fig. 5).

Female Survivorship l(x)

By definition female survivorship is the number of females surviving at the beginning of each age-class to lay eggs, which obviously is difficult to estimate for termites. But by a recursive process it may be assumed that the survival potential of the female is highest soon after she casts off the wings for a subterranean existence and it decreases proportionately with age. The theoretical probability of survival is estimated from the recurring series,

$$P_x = \frac{1}{2} P_{x-1} + \frac{1}{4} P_{x-n}, \quad \dots 4$$

the sequence being related by

$$P_x = a_1 P_{x-1} + a_2 P_{x-2} \quad \dots 5$$

where *a* is the mortality constant for different age-groups, *P* the probability of survival at different age-classes (*x*). Assuming a freshly de-alate female has a survival potential of 1.00, the survival schedule for the subsequent age-classes estimated by use of Eq. 4 is shown in Fig. 5.

Age-Specific Fecundity m(x)

In general, the females of different age-groups show a progressive development in the number of ovarioles : histochemical characteristics of these ovarioles also change with age and stages of development (Banerjee, 1964). Consequently,

the number of eggs present varies with age as reflected by the size of the queen (Fig 3). Statistically, a highly significant relationship ($b = 0.92$ $P < 0.01$) exists between the size, reflecting the age of the queen, and the number of ovarioles: the regression equation and fitted regression line are shown in Fig 4. The number of eggs in a female can therefore be considered to be an acceptable axiom for age-specific fecundity (Fig 5).

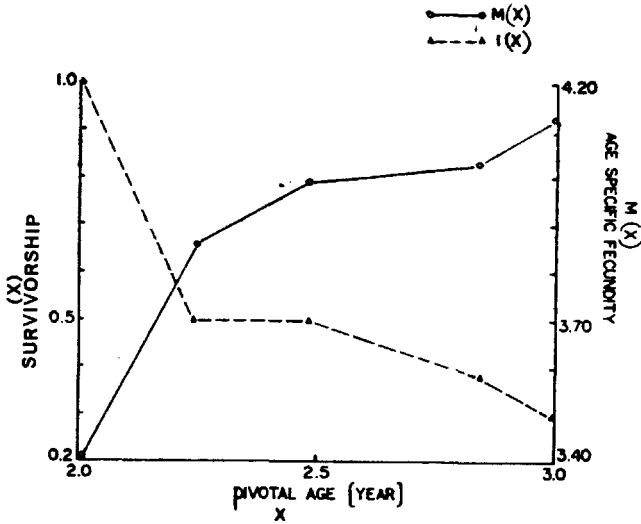


FIG. 5. Population growth characteristics of *Odontotermes redemanni* (Wasmann).

Intrinsic Rate of Increase, r_m

Having computed the parameters (x) , $l(x)$ and $m(x)$, the best numerical solution of Eq. 3 is obtained with a value of r_m 0.96. The steps in the numerical solution of the equation are shown in Table I. Eq. 3 can now be approximated to

$$\sum e^{-0.96 x} l(x) m(x) = 1.00 \quad \dots 6$$

The finite rate of increase, i.e. the number of times the population multiplies in unit time is then estimated from the relationship,

$$\lambda = e^{r_m} \quad \dots 7$$

Solving the equation, we find *O. redemanni* population grows at the rate of 2.61 individuals per head per year or 0.007 individual per head per day.

Net Reproductive Rate R_0

The net reproductive rate is the factor by which the population increases in one generation. This is given by

$$R_0 = \sum_0^{\alpha} l(x) m(x) \quad \dots 8$$

$$= \sum_0^{\alpha} V_x = 10.02 \quad \dots 9$$

On theoretical ground $R_0 > 1$ is the characteristic of a growing population and $R_0 < 1$ is the characteristic of a declining one. Obviously, the phase of the population considered here is in the state of rapid expansion, indicating that colonies are still young and activity proliferating their populations.

Gross Reproductive Rate (GRR)

This is the average reproduction of the female which survives through all age-groups computed as

$$GRR = \sum m(x) \quad \dots 10$$

$$= 19.17$$

Unlike r_0 , R_0 and GRR are dependent on the specific behaviour of age-groups. Consequently, they may reflect certain bias towards some age-groups.

Growth Equation for Termite

The exponential growth rate of *Odontotermes redemanni* is expressed (Banerjee, 1971) as

$$Nt_2 = Nt_1 e^{(r-r_3) K(t_2-t_1)}, \quad \dots 11$$

where $r = r_m$, r_s is the intrinsic requirement of different castes in a colony, and K is the developmental rate of the eggs which is about three months (Mukerji & Mitra, 1948; Mukerji, 1970). Provided r_s is known, equation 11 can be restated as

$$Nt_2 = Nt_1 e^{(0.96-r_3) 3(t_2-t_1)}, \quad \dots 12$$

Once all the variables are sorted out Eq. 11 can be integrated to

$$Nt_2 = Nt_1 e^{0.96t} \quad \dots 13$$

The theoretical level of population expected from growth coefficient may be considerably higher than the observed level (Banerjee, 1966 b). This is to be expected because r_m is essentially an index of growth potential : in practice, the population may show wide variability and deviate from expected level, depending on the interactions between K and r_s in Eq. 11.

DISCUSSION

Demographic data on the population production by termites are rare: this precludes a direct comparison of the data on *Odontotermes redemanni* with that of other species. However, some information is available on social insects other than termites (Brian, 1965; Wilson 1972). The growth rate of ant *Myrmica*, for example is 0.001 individual per head per day, while that of *Aphis*, *Bombus*, and *Vespula* is 0.03, 0.03, and 0.05 per head per day respectively. Polybiine wasps with a growth rate of 0.1 individual/individual/day have a much higher population production rate than that of any other social insect.

Neotermes tectonae is the only species of termite with a known intrinsic rate of increase (Lee & Wood, 1971): young colonies of *N. tectonae* increase at the rate of 1.66/individuals/individual/year (0.004 individual/individual/day) while the older colonies have a slower growth rate of 0.57/individual/individual/year (0.001 individual/individual/day). Although in the case of *O. redemanni* a differential growth rate could not be established, a finite rate of increase of 0.007 individual/individual/day is definitely on the lower side and confirms the general slow growth rate of the mounds (Banerjee, 1975). For *O. redemanni*, with its ability to lay about 17,820 eggs a day (Escherich, 1911), the demographic growth rate is very slow indeed, but the productivity of the colonies is possibly best judged from the functional production of adults of different castes, rather than the production of eggs.

Even with its fairly low growth coefficient, populations of *O. redemanni* will continue to grow exponentially unless a damping factor is introduced. Moreover, since intrinsic rate of increase is a constant, exponential equation will not indicate the rate of population change in the absence of this damping factor. In practice, *O. redemanni* populations may not increase exponentially indefinitely — the functional requirements of the colony, particularly the need for the production of adults of different castes, exert a sort of damping effect on the population (Banerjee, 1971).

TABLE I

Steps in the calculation of the intrinsic rate of increase for Odontotermes redemanni (Wasmann)

x	$l(x)$	$m(x)$	$r_m(x)$	$e^{-r_m(x)}$	$l(x)m(x)$	$e^{-r_m(x)}l(x)m(x)$
2.00	1.00	3.37	1.92	0.14	3.37	0.47
2.24	0.50	3.86	2.15	0.11	1.93	0.21
2.48	0.50	3.89	2.38	0.09	1.95	0.18
2.85	0.38	3.93	2.74	0.06	1.49	0.09
3.15	0.31	4.12	3.02	0.04	1.28	0.05
						Σ 1.00

In termite colonies, as in other social insects, the female or queen is the unit of selection (Wilson, 1972); therefore colony fitness is measured either from queen survivorship [$l(x)$] or queen fecundity [$m(x)$]. A low survivorship is compensated for by high fecundity and vice versa. It is, however, not known if the behavioural or physiological processes that regulate this trend in *O. redemanni*, are the same as in other social insects, though on theoretical ground they may be considered to be so (Wilson, 1972).

In general, amongst all social insects, termites and ants have the lowest population growth coefficient, and the wasps the highest, with bees occupying an intermediate position. These differential growth coefficients reflect the productive requirements of the colonies, rather than common or rareness of the species.

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