

# Functional and numerical responses of the predatory bug *Macrolophus caliginosus* Wagner fed on different densities of eggs of the greenhouse whitefly, *Trialeurodes vaporariorum* (Westwood)

ABDUL-JALIL SALEM HAMDAN

Department of Plant Production and Protection, Faculty of Agriculture,  
Hebron University, Hebron P.O. Box 40, Palestine

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Laboratory experiments under standard conditions (25 °C, 50-75% relative humidity, 16:8 L:D) were conducted to determine the functional and numerical responses of the adult female of *Macrolophus caliginosus* to different densities of the greenhouse whitefly on tobacco leaf discs. The results showed that the functional response of *M. caliginosus* was density-dependent with regard to the consumption of *Trialeurodes vaporariorum* eggs at different prey densities, up to 300 *T. vaporariorum* eggs/arena/day. This response fitted the type III functional response. The numerical response of *M. caliginosus* was positively related to prey density, with more oocytes per female, a higher age-specific fecundity and higher intrinsic rate of increase at high prey densities than medium or low prey densities.

**Key words:** *Macrolophus caliginosus*, *Trialeurodes vaporariorum*, functional response, numerical response.

## INTRODUCTION

To describe the nature of predation, two terms were initially proposed by Solomon (1949), namely the functional response, which is defined as the change in attack rate per predator with variation in prey density, and the numerical response, which is the change in predator numbers with variation in prey density. Holling (1959a, b) suggested that Solomon's functional response could be further subdivided into three types: type I, in which prey consumption increases linearly to a plateau with increasing prey density; type II, in which prey consumption increases asymptotically to a plateau with increasing prey density, and type III, in which prey consumption is S-shaped (sigmoid) with increasing prey density.

Later on, Bell (1991) and van Alphen & Jervis (1996) suggested four types of functional responses as follows:

- Type I: where there is a rectilinear rise to the maximum in the number of prey eaten per predator as the prey density increases;
- Type II: where the response rises at a constantly decreasing rate towards a maximum value, i.e. the response is curvilinear up to the asymptote, in contrast to the Type I response;
- Type III: where the response resembles the Type II response except that it accelerates at lower prey densities, the response is thus sigmoid, and
- Type IV: where the response resembles the Type II response except that at higher densities it declines, producing a dome-shape.

A method for determining the functional response was described by van Alphen & Jervis (1996) as follows:

1. Individual insects to be confined in an arena (e.g., cage) with different numbers of prey or hosts, for a fixed period of time.
2. At the end of the experiment, the natural enemies are removed and, in the case of predators, the

\* Corresponding author: tel.: +972 (02) 2220995 (ext. 166), fax: +972 (02) 2229303, e-mail: [ajhamdan@hebron.edu](mailto:ajhamdan@hebron.edu)

number of prey killed is counted.

3. From the counts, a graph can then be plotted relating the number of prey attacked to the number offered.
4. The plot is then compared with the functional response curves (Holling, 1959a, 1961, 1966; Rogers, 1972; Royama, 1977; Mills, 1982; Arditi, 1983; Casas *et al.*, 1993).

Foglar *et al.* (1990) studied the functional response of *Macrolophus caliginosus* with two prey species, *M. persicae* and *M. urticae*, and found that, with both prey species, *M. caliginosus* showed a Holling's type II response. However, Abdel-Aziz (1994) studied the functional responses of *M. caliginosus* when fed on *Trialeurodes vaporariorum* stages offered on both tomato and cucumber, and he concluded that the functional response of *M. caliginosus* fitted a type II Holling's functional response curve when offered immature stages of *T. vaporariorum*, whereas the predator had no or only a very low response to *T. vaporariorum* adults. Further analysis of Abdel-Aziz data showed that the functional response of *M. caliginosus* actually fitted a type III curve described by van Alphen & Jervis (Hamdan, 1997). Latest studies on the functional response of *M. caliginosus* to whiteflies and spider mites showed that predation of the *M. caliginosus* female presented with first instars of greenhouse whitefly was a type III functional response (Enkegaard *et al.*, 2001).

The objective of this experiment was to examine the functional and numerical responses of adult female *M. caliginosus* to different densities of greenhouse whitefly eggs on tobacco leaf discs.

## MATERIALS AND METHODS

A culture of *M. caliginosus* Wagner was established using 500 specimens provided by the Biological Crop Protection Ltd. (BCP) at Wye, Kent, UK. The *M. caliginosus* culture was reared on tobacco plants infested with *T. vaporariorum* (Westwood), and kept in a growth room chamber under standardised conditions of 25°C, 16:8 L:D photoperiod and of 50 - 70% relative humidity (RH). All plants with or without insects were kept inside perspex culture cages (60 × 40 × 50 cm, length × width × height) on wet capillary matting on trays.

A group of 150 (one day-old) adults of *M. caliginosus* were released onto a tobacco plant heavily infested with eggs of the greenhouse whitefly (GHWF), *T. vaporariorum*. They were kept for two days in a

ventilated perspex cage 40 × 50 × 60 cm in a growth chamber under standardised conditions (25°C, 50-75% RH, 16:8 L:D) to ensure copulation. On the third day, each *M. caliginosus* female was reared separately in 5 cm diameter Petri dish cages and offered a clean tobacco leaf disc for a fasting period of 24 h before starting the feeding regimes. Then, six prey density treatments were offered daily: 0, 10, 50, 100, 200 and 300 GHWF eggs/arena/day.

Two types of leaf discs were offered in each cage, one for food and another for oviposition prepared as follows:

- a) 2 cm diameter tobacco leaf discs infested with the proper number of GHWF eggs as food without leaf-veins, and
- b) 5 cm diameter clean tobacco leaf discs + *Pelargonium* leaf offered as oviposition site, each leaf with a midrib and/or thick veins suitable for oviposition.

Each predator was moved to freshly prepared cages every day, and the daily consumption of each replicate was recorded. All cages were kept under the standardised conditions for the incubation period and the number of nymphs emerging from each cage was recorded.

In each prey density-treatment, ten adult females were used. After one week, all live *M. caliginosus* females were weighed: four females from each treatment were placed in plastic vials and kept in a freezer for later dissection in order to determine the effect of the different prey densities on the number of developed oocytes in the ovarioles of each female. The other *M. caliginosus* females were left to continue feeding on the same prey density until death.

The life table parameters were calculated using the QBasic program (Jervis & Copland, 1996) (Appendix). Hence, this experiment started with adult stages and, therefore, the analyses were done on the basis of the results obtained by Hamdan (1997) who found nymph survival of 86% and adult eclosion at age of 27 days with a female percentage of 39% (14:22 F:M).

The data used from this experiment to calculate the life table parameters included the age-specific fecundity, the proportion of survival during the adult stage and the calculated age-specific "fertility" of *M. caliginosus* female during its adult life.

## RESULTS

### Functional response

The average number of GHWF eggs consumed per *M. caliginosus* female increased significantly with in-

TABLE 1. Numbers and percentages of GHWF eggs consumed by *Macrolophus caliginosus* females fed on different prey densities (means  $\pm$  se\*\*)

Prey density (n*) (GHWF eggs/cage/day)	Number of GHWF eggs consumed/day	% of GHWF eggs consumed***
0 (21)	0.0 <sup>d</sup>	0.0 <sup>e</sup>
10 (52)	7.1 $\pm$ 0.452 <sup>d</sup>	70.8 $\pm$ 4.52 <sup>b</sup>
50 (54)	40.7 $\pm$ 2.04 <sup>c</sup>	81.3 $\pm$ 4.08 <sup>a</sup>
100 (75)	67.3 $\pm$ 3.24 <sup>b</sup>	67.3 $\pm$ 3.24 <sup>b</sup>
200 (43)	92.1 $\pm$ 3.91 <sup>a</sup>	46.0 $\pm$ 1.95 <sup>c</sup>
300 (55)	93.5 $\pm$ 4.82 <sup>a</sup>	31.2 $\pm$ 1.61 <sup>d</sup>
<i>p</i> value	$< 10^{-3}$	$< 10^{-3}$

\* = n: number of replications (days)

\*\* = means within the same column with different letters differ significantly at the 0.001 level (one way ANOVA, Tukey's family error rate)

\*\*\* = se calculated from the equation  $se = 100\sqrt{pq}/n$ , where  $p$  = proportion consumed,  $q = 1-p$

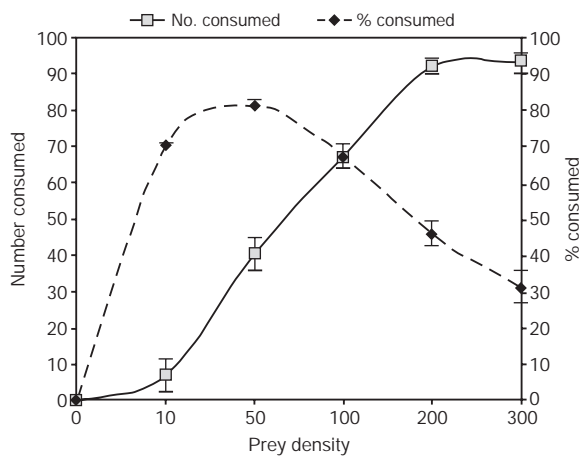


FIG. 1. Functional response of *Macrolophus caliginosus* fed on GHWF eggs.

creasing prey density within the range of 0-200 GHWF eggs/arena/day, above which the daily consumption was stable and without any significant increase (Table 1 and Fig. 1). However, the proportion consumed tended to increase with increasing prey density, reaching a maximum of 81% at 50 GHWF eggs/arena/day, after which it decreased at higher densities (Table 1).

Results in Fig. 1, showed that the functional response of *M. caliginosus* to increasing densities of GHWF eggs fitted a type III functional response, which was recently described by van Alphen & Jarvis (1996). This response resembles the Holling's (1959a) type II, except that, at lower prey densities, the percentage consumed accelerated to reach a peak at a prey density over 50 GHWF egg/arena/day before starting to decline at higher densities.

#### Numerical response

The results in Table 2 show the effect of prey density on adult longevity, oviposition period, and total nymphs produced and average nymphs/female/day during the oviposition period. These parameters tended to increase with increasing prey density but this effect was not significant. *Macrolophus caliginosus* females survived on the control treatment (0 GHWF egg/day) for an average of 12.5 days, presumably feeding on plant juice, and produced an average of seven nymphs per female.

On the other hand, when the analyses were done on the basis of three prey density ranges i.e., low density ranging from 0 to 10 GHWF eggs/arena/day, medium density ranging from 50 to 100 GHWF eggs/arena/day and high density ranging from 200 to 300 GHWF eggs/arena/day, the results in Table 3 show that, the adult weight, number of developed oocytes/female, number of offspring produced during the first 10 days and the mean number of offspring produced/female, are all significantly higher when fed on medium and high prey density than fed on low prey density.

The results in Fig. 2 show that the cumulative number of nymphs/female tended to increase with increasing prey density and the oviposition period of the *M. caliginosus* females offered a high prey density (200-300 GHWF eggs/arena/day), double that of the females offered medium or low prey density ( $< 100$  GHWF eggs/arena/day).

Fig. 3 shows that the "fertility" of *M. caliginosus* increased with increasing prey density, with a significantly higher age-specific fecundity and a longer ovi-

TABLE 2. Adult longevity and number of nymphs emerged/female fed on different prey density treatments (means  $\pm$  se; n\* = 6)

Prey density/day (GHWF eggs)	Adult longevity (days)	Oviposition period (days)	Average number of nymphs/female	Mean number of nymphs/female/day of oviposition period
0	12.5 $\pm$ 1.48	5.7 $\pm$ 1.54	7.0 $\pm$ 2.19	1.2 $\pm$ 0.37
10	10.3 $\pm$ 1.23	4.3 $\pm$ 1.65	9.0 $\pm$ 3.26	1.9 $\pm$ 0.42
50	12.3 $\pm$ 2.08	4.7 $\pm$ 2.55	11.0 $\pm$ 6.07	1.3 $\pm$ 0.61
100	13.8 $\pm$ 2.44	5.0 $\pm$ 2.13	14.8 $\pm$ 7.31	1.7 $\pm$ 0.68
200-300	15.5 $\pm$ 2.78	9.8 $\pm$ 3.34	31.7 $\pm$ 15.6	2.4 $\pm$ 1.04
<i>p</i> value**	0.509	0.462	0.259	0.730

\* = n: number of replications

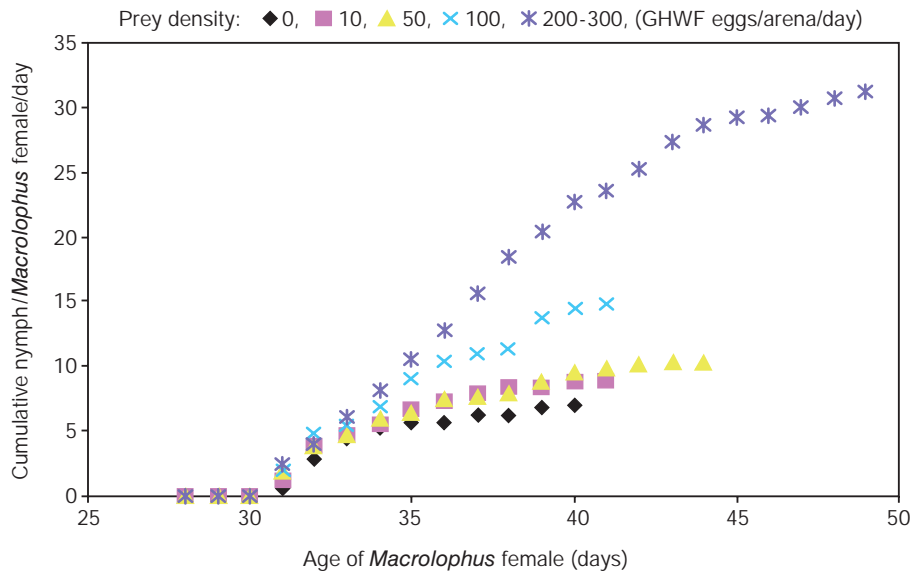
\*\* = *p* value for comparison between different densities (one way ANOVA, Tukey's family error rate)

FIG. 2. Cumulative number of offspring/female/day when females fed on prey densities of 0, 10, 50, 100 and 200-300 GHWF eggs/arena/day.

TABLE 3. Effect of prey density on adult weight and fertility of *Macrolophus caliginosus* (means  $\pm$  se\*)

Prey density range GHWF eggs/arena/day	Adult weight at day 10 (mg)	Number of oocytes/ female on day 10	Mean nymphs/female/ 1 <sup>st</sup> week of oviposition	Mean nymphs/ adult period
Low density < 10	0.899 <sup>b</sup> $\pm$ 0.020 (15)	1.5 <sup>b</sup> $\pm$ 0.327 (8)	7.6 <sup>b</sup> $\pm$ 1.12 (20)	8.0 <sup>b</sup> $\pm$ 1.89 (12)
Medium density 50-100	1.112 <sup>a</sup> $\pm$ 0.042 (17)	3.87 <sup>a</sup> $\pm$ 0.693 (8)	11.2 <sup>ab</sup> $\pm$ 2.7 (20)	12.9 <sup>ab</sup> $\pm$ 4.57 (12)
High density 200-300	1.193 <sup>a</sup> $\pm$ 0.053 (9)	4.75 <sup>a</sup> $\pm$ 1.25 (4)	21.1 <sup>a</sup> $\pm$ 7.4 (10)	31.7 <sup>a</sup> $\pm$ 15.6 (6)
<i>p</i> value	< 10 <sup>-3</sup>	0.011	0.037	0.0069

\* = means within the same column with different letters differ significantly at the 0.05 level (one way ANOVA, Tukey's family error rate)

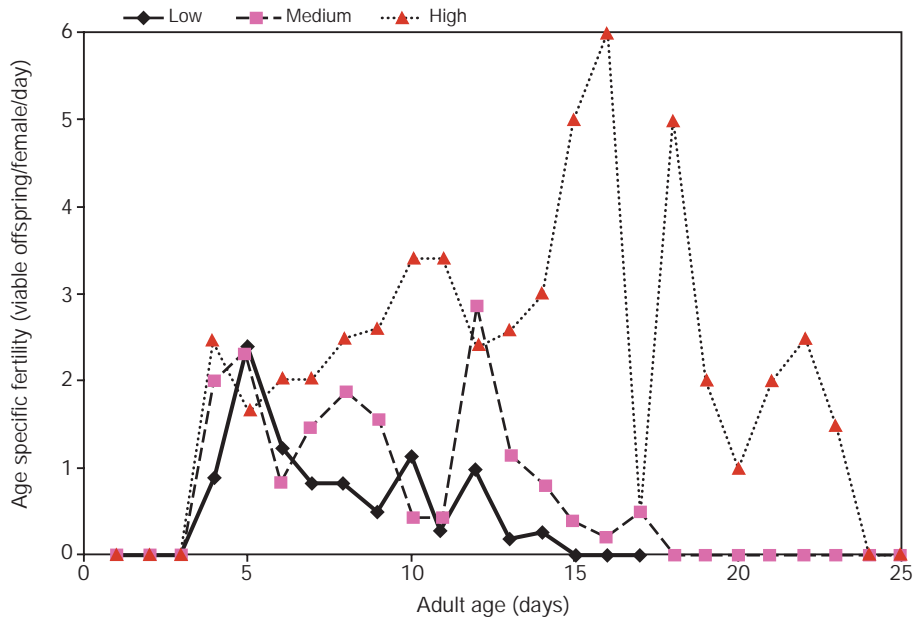


FIG. 3. Number of viable offspring produced/female/day when fed either on low, medium or high prey density.

position period at the higher densities. The oviposition period increased with increasing prey densities and reached 14 days on low, 17 days on medium and 23 days on high prey densities. Furthermore, one peak of eggs laid/female fed on low prey density occurred on day 5, two peaks when fed on medium prey density occurred on day 5 and on day 12 and five peaks when fed on high prey density occurred on day 4, 10, 15, 17 and 22.

*Life table*

The results in Table 4 show that the life table parameters were affected by the prey density range. The gross reproductive rate (GRR), the net reproductive rate (Ro), the capacity for increase (rc), the intrinsic rate of increase (rm), the cohort generation time (Tc), the generation time (T) and the finite capacity for increase (l) were all increased in proportion to the increasing prey density, whilst the doubling time (DT) declined with increasing prey density.

TABLE 4. Life table parameters\* of *Macrolophus caliginosus* fed on either a low, medium or high prey density of GHWF eggs

Life table parameters	Prey density range (GHWF eggs/arena/day)		
	Low (< 10)	Medium (50-100)	High (200-300)
GRR	4.8	8.4	27.6
Ro	3.4	5.4	13.4
rc	0.03754481	0.0496974	0.0696475
rm	0.03767337	0.0500907	0.0726776
Tc	32.8	34.0	37.3
T	32.7	33.7	36.5
l	1.038392	1.051366	1.07869
DT	18.4	13.8	9.7

\* = life table parameters: GRR, gross reproductive rate; Ro, net reproductive rate; rc, capacity for increase; rm, intrinsic rate of increase; Tc, cohort generation time; T, generation time; l, finite capacity for increase; DT, doubling time

## DISCUSSION

### Functional response

*Macrolophus caliginosus* shows significant responses to different densities of GHWF eggs. The results of the current study resemble those by Enkegaard *et al.* (2001) who found that predation of *M. caliginosus* fed on GHWF fits type III functional response.

In previous studies, Foglar *et al.* (1990) and Abdel-Aziz (1994) reported that the functional response of *M. caliginosus* females showed a type II Holling's response (Holling, 1959a) when reared on either *M. persicae*, *M. urticae* (Foglar *et al.*, 1990) or *T. vaporariorum* (Abdel-Aziz, 1994). Although, Abdel-Aziz (1994) determined the functional responses by comparing the curves for the number of prey consumed with increasing densities using the Holling's type responses, he did not discuss the proportion consumed. Hamdan (1997) suggested that further analysis of Abdel-Aziz data, using the curves for the proportion consumed in addition to the curves of the numbers consumed showed that the data also fit to type III responses of van Alphen & Jervis (1996). In conclusion, the complete analysis of the data by Abdel-Aziz (1994) is in agreement with the results of the present study.

It seems possible that the type of response is related to prey size, with a type III response for small prey and, type II for larger prey. Hassell *et al.* (1977) reported that *Notonecta glauca* L. (Hemiptera) preying on *Asellus aquaticus* L. (Isoptera) had a type III response for small (3-5 mm) *A. aquaticus*, and a type II response for larger individuals (7-9 mm). The same authors also reported that *Coccinella septempunctata* L. (Coleoptera) also produced a type III functional response when foraging for first instar cabbage aphid *Brevicoryne brassicae* L. (Aphididae) and a type II response when foraging for fifth instar. Streams (1994) concluded that the prey size might affect the functional response of the predator and that the predator could have a type II functional response on larger prey and a type III on smaller prey. Therefore, it can be concluded that the functional response of *M. caliginosus* fits a type III when foraging for small prey, such as GHWF and a type II when foraging for larger prey, such as *M. persicae* (Hamdan, 1997).

### Numerical response

*Macrolophus caliginosus* showed a significant increase in body weight and in the number of developed oocy-

tes/female (one week after the introduction of the different feeding regimes). These increases were proportional to the increase in prey density. In addition, adult longevity, age-specific fecundity and the cumulative number of nymphs produced/female also increased in proportion to the increase in prey density. Thus, five peaks of egg oviposition occurred when *M. caliginosus* females were fed on high prey density, two peaks on medium prey density and only one peak on low prey density. This shows that when a satisfactory food was available, more oocytes developed and the oviposition period was longer. Therefore, the intrinsic rate of increase was positively correlated with the increasing prey density, resulting in a proportional decrease in the doubling time of the *M. caliginosus* population.

The present study shows that *M. caliginosus* showed a positive numerical response to prey density. When foraging at high prey densities, *M. caliginosus* tended to have high rates of increase, to survive for longer, to produce more nymphs and to double its population more quickly than when foraging at medium or low prey densities. In addition, it was found that when *M. caliginosus* adults were released, they were able to survive and to produce offspring even in the absence of insect prey.

The effects of prey density on the numerical response of *M. caliginosus* were in general agreement with the responses of other heteropteran predators fed at varying prey densities. In particular, with *Anthocoris confusus* fed on the aphid *Aulacorthum circumflexus* (Buckton) (Evans, 1976), with *Podisus maculiventris* fed on *Tenebrio molitor* L. (O'Neil & Wiedenmann, 1990; Wiedenmann & O'Neil, 1990), and with *Podisus maculiventris* given low numbers of *Epilachna varivestis* Mulsant as a prey (Legaspi & O'Neil, 1993, 1994).

## CONCLUSIONS

1. The functional response of *M. caliginosus* is density-dependent with regard to the consumption of GHWF eggs at different prey densities up to 200 GHWF eggs/arena/day. This response fitted the type III functional response described by van Alphen & Jervis (1996).
2. The numerical response of *M. caliginosus* was positively related to prey density, with higher adult weight, more oocytes per female, a longer period of oviposition, a longer period of adult survival, a higher age-specific fecundity, a higher intrinsic

rate of increase and a shorter doubling time at high prey densities than medium or low prey densities.

3. *Macrolophus caliginosus* has the ability to survive and produce offspring when released as adult, even in the absence of prey.

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Appendix: QBasic program for the calculation of life table parameters (c.f. Jervis & Copland, 1996)

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10 REM program to calculate life table parameters (MJWC 1996)
15 CLS
20 DIM x(100), k(100), m(100): REM dimension arrays (n < 100)
30 READ n
35 FOR h = 1 TO n: READ x(h), k(h), m(h): NEXT h: REM read data
40 PRINT "calculating data"
50 ct = 0: mx = 0: ro = 0: j = 1: REM set variables
60 REM ----- cumulative calculations
70 FOR h = 1 TO n
80 ct = ct + x(h) * k(h) * m(h): mx = mx + m(h): ro = ro + k(h) * m(h)
90 NEXT h
100 rc = LOG(ro) / (ct / ro): rm = rc: REM calculate rc
110 crm = 0: FOR h = 1 TO n
115 crm = crm + k(h) * m(h) * EXP(-x(h) * rm): NEXT h
120 REM ----- iterative substitution for rm
130 IF ABS(1 - crm) < .00001 THEN GOTO 180: REM accurate to 4 dec points
140 IF crm > 1 THEN rm = rm + ABS(1 - crm) / x(1)
150 IF crm < 1 THEN rm = rm - ABS(1 - crm) / x(1)
160 PRINT j: j = j + 1: GOTO 110
170 REM ----- display results
180 PRINT "gross reproductive rate (GRR) =": mx
190 PRINT "net reproductive rate (Ro) =": ro
200 PRINT "capacity for increase (rc) =": rc
210 PRINT "intrinsic rate of increase (rm) =": rm
220 PRINT "cohort generation time (Tc) =": ct / ro
230 PRINT "generation time (T) =": LOG(ro) / rm
240 PRINT "finite capacity for increase (lambda) =": EXP(rm)
250 PRINT "doubling time (DT) =": LOG(2) / rm
260 END
270 REM
280 REM ----- data
290 DATA 23: REM number of days data
300 DATA 27, .86, .00: REM x (day), lx (survival), mx (fecundity)
310 DATA 28, .86, .00: REM female offspring

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