Theoretical Estimates of Consumable Food and Probability of Acquiring Food in Larvae of *Chrysomya putoria* (Diptera: Calliphoridae)

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An indirect estimate of consumable food and probability of acquiring food in a blowfly species, Chrysomya putoria, *is presented. This alternative procedure combines three distinct models to estimate consumable food in the context of the exploitative competition experienced by immature individuals in blowfly populations. The relevant parameters are derived from data for pupal weight and survival and estimates of density-independent larval mortality in twenty different larval densities. As part of this procedure, the probability of acquiring food per unit of time and the time taken to exhaust the food supply are also calculated. The procedure employed here may be valuable for estimations in insects whose immature stages develop inside the food substrate, where it is difficult to partial out confounding effects such as separation of faeces. This procedure also has the advantage of taking into account the population dynamics of immatures living under crowded conditions, which are particularly characteristic of blowflies and other insects as well.*

Key words: *Chrysomya putoria* - density-independence - exploitative competition - consumable food - population dynamics

Knowledge of the nutritional requirements of insects and their interaction with food sources are basic for an understanding of their biology, since the amount and quality of food affect the growth rate at the immature stage and subsequent adult body size (Scriber & Slansky 1981, Farrar et al. 1989). In completely favorable environments the performance of each individual is genetically determined, which in turn determines its maximal fitness in nutritional terms (Slansky & Rodriguez 1987). Nevertheless, environmental factors including density dependent mechanisms may be responsible for constraints on the consumption, utilization and allocation of food (Nicholson 1954, Rodriguez 1988, Travis 1990), with attendant consequences for the dynamic behaviour of populations (Mueller 1988).

In calliphorid flies, the major period of resource limitation occurs during the larval stage, and their mode of competition for food is generally considered as the exploitative type, where the larvae scramble for food, each one trying independently to acquire as much food as possible before it is completely exhausted (Levot et al. 1979, Lomnicki 1988). Some larvae end up with more food than the minimal required for survival, others reach just the minimal amount, whereas some are not able to reach this minimal necessary for pupariation and die (de Jong 1976). The food eaten by the dead individuals is therefore wasted, and this situation is inherent to scramble competition when resource is in short supply (de Jong 1976, Levot et al. 1979, Lomnicki 1988).

The relative rate of consumption is a parameter commonly employed for quantifying the behavioural response of insects with respect to the food source (Waldbauer 1968), although in certain cases the outcome of larval competition for food is perhaps more closely approximated to larval assimilation than to true consumption (Putman 1977). Essential for studies of nutritional ecology are research techniques that employ biochemistry, physiology, genetics and behaviour of organisms (Slansky & Rodriguez 1987). Gravimetry has been used in several studies of food assimilation for distinct orders of insects (Waldbauer 1968, Holter 1982, Zheng et al. 1993). Other procedures may also be used such as some types of marker meth-

ods (Mcginnis & Kasting 1964, Holter 1973, Hanski 1976, Barbehenn 1993), chromic oxide (Holter 1973), radioactively labelled yeast (Miranda & Eggleston 1988), silicon markers (Barbehenn 1993) and the number of cephalopharingeous retractions during the larval feeding process (Mueller 1988).

The estimation of consumable food by all survivors through the above techniques is nevertheless very difficult to obtain in insects whose immature stages develop inside the food substrate, like blowflies, because larval faeces would make up part of food left over. This situation can impede the separation of faeces from the remaining substrate (Schumann 1971, Hanski 1976). Estimates of consumable food in insects whose larval stages are usually exposed to severe exploitative intraspecific competition must, by necessity, be made in a context of population dynamics.

Herein, we present an alternative method for theoretical estimation of consumable food by survivors until pupariation, in different larval densities of *Chrysomya putoria*, a blowfly recently introduced in Brazil (Guimarães et al. 1978) and associated with decomposing organic matter, mainly in urban areas (Linhares 1981, Guimarães 1984, d'Almeida & Lopes 1983, d'Almeida 1989, 1993). This species has considerable medical and sanitary importance, because it can be a mechanical vector of pathogens (Greenberg 1971), and also produce secondary myiasis in man and other animals (Zumpt 1965).

Our procedure combines three different models which address the problem of consumable food by the survivors in a context of population dynamics. This approach combines estimates of density-independent larval mortality (Morris 1990) to infer the amount of food consumable according to Ullyett (1950), using pupal weight and survival data. The key calculations are based on a theoretical mean value of efficiency of conversion of ingested food (ECI) obtained in saprophagous invertebrates by Heal (1974) (see review in Slansky & Scriber 1982). The probability of acquiring food per unit of time, the time in discrete units necessary for the larvae to attain the minimal pupal weight, and the time taken to exhaust the food supply were also calculated (de Jong 1976), because of their importance for organisms that compete for limited amounts of food such as the majority of larvae of calliphorid flies.

MATERIALS AND METHODS

Laboratory populations of Chrysomya putoria - Laboratory populations of *C. putoria* were founded from specimens collected from the campus of "Universidade Estadual de Campinas",

Campinas, São Paulo, Brazil, using carrion rodent baits. Adult flies were maintained in cages (30 x 30 x 48 cm) covered with a nylon mesh at $25\pm1°C$, 60% relative humidity and 12 hr photophase, being fed water and sugar *ad libitum*. Adult females were fed fresh beef liver to allow their complete gonotrophic cycle. Second laboratory generation (F_2) was used in experiments.

Estimation of consumable food by the survivors - The theoretical amount of consumable food was estimated by the model proposed by Ullyett (1950), asserting that a certain amount of food theoretically allows the development of a given number of individuals of maximum weight. However, Ullyett makes an assumption of a theoretically value of 100% of food conversion into biomass, which is very unrealistic. In the present study, we utilize an ECI of 39%, considered by Heal (1974) as a mean value for saprophagous invertebrates. For insects, such as blowflies, whose larvae experience competition for food, the maximum weight will, to a large extent, depend on the degree of larval crowding, which is known to impose constraints both in the number and weight of survivors. In this study maximum weight was measured at the pupal stage for a range of larval densities which reproduces the process of exploitative competition characteristic of blowflies (Godoy et al. 1993). Accordingly to adopted ECI, for a larva to attain a given weight as a pupa, it must feed an amount equivalent to 2.5641 times its pupal weight.

Twenty different larval densities ranging from 100 to 2,000 larvae with intervals of 100 were established using 50,000 mg of rearing medium per vial (7.2 cm diameter x 13.8 cm height), prepared according to Leal et al. (1982). These larval densities are equivalent from 2 to 40 individuals per g. The rearing medium was chosen in order to control the amount of protein content and to avoid extraneous variation that might be introduced with other media such as liver or carcass. Survival was estimated as the number of adults emerging per vial, and the mean number of adults was calculated from four replicate vials for densities of 100 to 500 larvae, three vials for densities of 600 to 900, two vials for densities of 1,000 to 1,300 and finally one vial for the remaining densities. Pupae totals were counted in each vial, and weights were estimated by weighing thirty pupae (nine days old) for each replicate in all densities, except for densities 1,400 and 1,500 where 23 pupae were weighed. The mean for number of pupae and pupal weight, and the values for minimal and maximum pupal weight were computed for each density.

The expected number of pupae of maximum weight that could be produced by the amount of food available is obtained by dividing the latter by

the maximal mean of pupal weight (multiplied by 2.5641) obtained for each density. Consequently, the unconsumable portion of food corresponded to the difference between the number of pupae expected if all food were consumed by the survivors and the number of pupae actually obtained experimentally for each density (Ullyett 1950).

The model by Ullyett (1950) requires an estimate of larval density-independent mortality, which is estimated here using the approach advanced by Morris (1990), following an earlier formulation due to Hassell et al. (1976). Hassell et al. (1976) proposed a method that can be used to estimate model parameters from population data, whose equation is written as

$$ln(N_t / N_s) = \beta ln(1 + \alpha N_t), \qquad (1)$$

where $N_s = N_{t+1}/\lambda$ is interpreted as the number of individuals surviving the density dependent stage in the life cycle whereas the number entering the stage is N_t. The maximum per-capita replacement rate per generation is written as λ and the parameters α and β determine how steeply the realized per-capita replacement rate declines in response to increasing larval density. The term on the left size of the equation define the *"k value"* (Varley & Gradwell 1960) associated with mortality during the density-dependent stage.

Morris (1990) modified this approach slightly, allowing density-independent mortality in the density-dependent stage by performing a non-linear regression of *k*-value mortality against density using the following modified version of the equation (1)

$$k = ln(N_t / N_s) = \beta ln(1 + \alpha N_t) \; ln\gamma, \qquad (2)$$

where γ represents density-independent mortality, subject to the constraint that $\gamma \leq 1$. Table II shows the mean percentage of individuals surviving in the replicates utilized to fit the parameters necessary for the computation of γ. Error estimates were obtained for each parameter. All estimates were performed by non-linear regressions using NLIN module of the SAS-PC (SAS Institute 1988), which uses a Newton algorithm to search for best-fit parameters.

Estimation of probability of acquiring food per unit of time and time taken to exhaust food (de Jong 1976) - (1) One type of food is present for which *n* larvae compete. A finite amount of particles of food (*M*) in mg is present; (2) A minimal quantity in mg (*m*) has to be eaten for a larvae to become adult; (3) Time can be counted in discrete units and is measured arbitrarily; in 1 time unit a larva eats either one or no food particles; (4) A larva eats at least the equivalent to the weight it will attain as a pupa (multiplied by 2.5641), to complete its de-

velopment; (5) The time of exhaustion of food in discrete units is *t* and *T* is the maximum time of the larval stage; (6) The probability per time unit (*P*) that a larva is feeding represents the average probability of acquiring food per time unit during the complete larval stage.

The time *t* taken to exhaust food equals the total number of food particles divided by the number eaten per time unit, and rounded to the nearest integer (*int*):

$$t = int\left(\frac{M}{P.n} + 05\right). \qquad (3)$$

It follows from assumptions 3 and 4 that the maximum amount of food a larva can possibly acquire is equal either to *t*, in the case of exhaustion of food, or to *T*, in the case of plentiful food supply. The probability of a larva eating *x* food particles is, according to the binomial distribution:

$$P(x) = \binom{t}{x} P^x (1-P)^{t-x}, \; x \leq t \leq T. \qquad (4)$$

For survival of a larva into adulthood it is necessary that $x \geq m$. The probability of survival or viability *v* is equal to the probability of acquiring any number of food particles *i* with $m \leq i$, $i \leq t \leq T$,

$$v = \sum_{i=m}^{i=t} \binom{t}{i} P^i (1-P)^{t-i}, \; t \leq T. \qquad (5)$$

The mean amount of food eaten by each survivor, *E*, is:

$$E\{i \mid i \geq m\} = \frac{1}{v} \sum_{i=m}^{i=t} i \binom{t}{i} P^i (1-P)^{t-i}, \; t \leq T. \quad (6)$$

The total amount of consumable food by the survivors, *B*, is given using equations (5) and (6):

$$B = n.v.E \qquad (7)$$

The best fitting values for the above parameters were obtained through simulations using MATLAB (1987).

RESULTS

Theoretical estimates of consumable food by the survivors, used in this study in *C. putoria*, require data on pupal weight and survival rates (Ullyett 1950). The minimal, maximum, and mean pupal weights, the minimal/maximum pupal weight ratio, and the survival rates of *C. putoria* in densities ranging from 100 to 2,000 larvae are given in Table I, and the mean number of pupae in each of the densities is demonstrated in Table II. In the context of the present study the maximum mean weight of the pupae is of particular interest because (1) it varies with larval density and (2) this value is necessary for the computation of the maximum amount of consumable food by the survivors for

TABLE I

Mean and standard deviation (SD), minimal and maximum values, and minimal/maximum ratios for pupal weight (mg) for *Chrysomya putoria* in 20 larval densities

| Density | Pupal weight | | Weight | | Minimal maximum |
	N	Mean ± SD	minimal	maximum	ratio
100	120	32.49 ± 10.68	3.9	55.3	0.07
200	120	35.85 ± 4.36	19.9	45.5	0.44
300	120	39.85 ± 6.33	18.8	52.3	0.36
400	120	36.59 ± 4.89	19.6	47.4	0.41
500	120	36.26 ± 4.85	20.5	47.5	0.43
600	90	32.82 ± 4.54	22.6	41.6	0.54
700	90	26.04 ± 4.55	13	38	0.34
800	90	20.26 ± 3.41	11.2	30	0.37
900	90	25.06 ± 5.04	11.8	38.2	0.31
1000	60	24.50 ± 6.18	12	37.6	0.32
1100	60	19.63 ± 5.44	9.6	30.9	0.31
1200	60	13.87 ± 4.03	4.1	24.4	0.17
1300	60	20.04 ± 5.45	10.5	31.5	0.33
1400	23	12.86 ± 2.56	9.9	21.7	0.46
1500	23	13.76 ± 3.55	6.8	22.5	0.30
1600	30	22.56 ± 3.85	10	29.7	0.34
1700	30	14.35 ± 2.69	7.9	20	0.39
1800	30	19.70 ± 3.82	13	27.2	0.48
1900	30	10.68 ± 1.86	7.9	14.7	0.54
2000	30	10.75 ± 2.90	2.2	17.3	0.13

TABLE II

Mean and standard deviation (SD) for percentage survival and total number of pupae of *Chrysomya putoria* in 20 larval densities

| Density | Percent survival | | Number of pupae | |
	N	Mean ± SD	N	Mean ± SD
100	4	73.25 ± 3.86	4	90.50 ± 7.50
200	4	70.12 ± 5.08	4	146.25 ± 7.89
300	4	39.66 ± 5.47	4	130.00 ± 15.64
400	4	40.12 ± 5.21	4	170.00 ± 27.47
500	4	44.70 ± 5.29	4	239.75 ± 18.67
600	3	45.05 ± 8.44	3	282.66 ± 54.42
700	3	52.95 ± 2.06	3	378.00 ± 12.16
800	3	52.41 ± 1.82	3	432.66 ± 15.04
900	3	38.92 ± 3.52	3	368.00 ± 32.07
1000	2	25.10 ± 4.24	2	261.50 ± 41.72
1100	2	20.95 ± 3.66	2	248.00 ± 31.11
1200	2	19.41 ± 2.24	2	284.50 ± 28.99
1300	2	25.38 ± 1.08	2	356.00 ± 18.38
1400	1	9.35	1	149.00
1500	1	10.93	1	195.00
1600	1	7.18	1	126.00
1700	1	13.64	1	298.00
1800	1	18.00	1	349.00
1900	1	7.94	1	153.00
2000	1	4.65	1	105.00

each larval density. For each larval density, the food available (50,000 mg) divided by mean maximum pupal weight (multiplied by 2.5641) yields a theoretical number of larvae of maximum weight that could be produced under optimal conditions.

Survival rates allow to partial out density-dependent and density-independent mortality factors according to Morris (1990), which are also necessary for the theoretical estimation of consumable food. During the larval stage, there was a density-independent mortality γ = 0.00612 ± 0.00092 corresponding to 0.6% mortality, considering all densities studied. It follows that the actual number of larvae of maximum weight that can be theoretically expected to develop in 50,000 mg of food is 0.6% *less* in all larval densities. For each density, multiplying the observed values of mean pupal weight (Table I) and number of pupae formed (Table II), and dividing by the maximum pupal weight (multiplied by 2.5641), it is possible to calculate the equivalent number of pupae if they were of maximum weight.

Hence, the unconsumable portion of food for each density is reflected in the difference between the maximum number of pupae expected if all food was consumed by the survivors, and that actually obtained. The theoretical amount of consumable food by the survivors in twenty larval densities of *C. putoria* can be obtained through the multiplication of the initial amount of food utilized per vial in the experiment (50,000 mg) by the percentage of pupae formed in relation to the maximum expected (Fig. 1). This figure shows that the higher values of amounts of consumable food corresponded to the densities of 500 to 900, 1,300 and 1,800 larvae.

Finally, the probability of acquiring food and the associated theoretical parameters were calculated for *C. putoria*, following de Jong (1976), using 50,000 mg of food for the development of the larval densities (*n*), and considering the values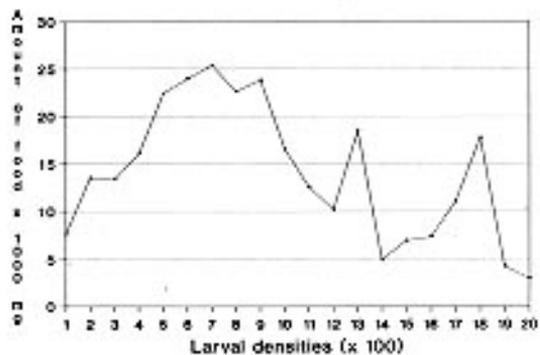 of consumable food previously obtained for each density (Fig. 1), as the parameter *B* in de Jong's model. The best fitted values of the probability of acquiring food per unit of time, the time in discrete units necessary for the larvae to attain the minimal pupal weight, and the time *t* taken to exhaust the food supply for the twenty larval densities of *C. putoria* are demonstrated in Figs 2, 3 and 4, respectively. The calculation of the time needed for the larvae to attain minimal pupal weight utilized the values of minimal pupal weight (Table I), whereas the calculation of time to exhaust food utilized the values of maximum pupal weight for each density (Table I). In comparison with the neighboring densities, higher values of probability of acquiring food are observed in the interval of 200 to 600 larvae, and also in the densities of 1,400 and 1,800 to 1,900 larvae (Fig. 2). The time taken for the larvae to attain the minimal pupal weight is larger in the densities of 200 to 600, 1,100, 1,300 to 1,400, 1,600 and 1,800 larvae, when compared with their respective neighboring densities (Fig. 3), whereas the time taken to exhaust the food supply increases with increasing larval densities (Fig. 4).

DISCUSSION

The data utilized here for the theoretical estimates of consumable food in *C. putoria* were obtained for a range of larval densities, which entails
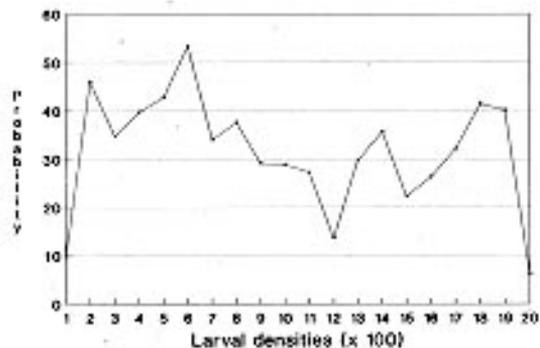

Fig. 2: probability of acquiring food per unit of time in *Chrysomya putoria* in 20 larval densities.

Fig. 1: theoretical amount of consumable food by larvae of *Chrysomya putoria* in 20 larval densities.
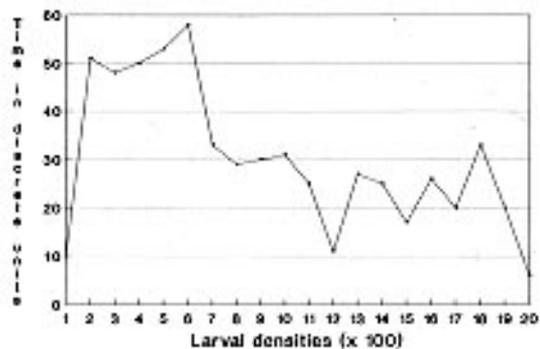

Fig. 3: time in discrete units necessary for larvae of *Chrysomya putoria* to achieve minimal pupal weight in 20 larval densities.
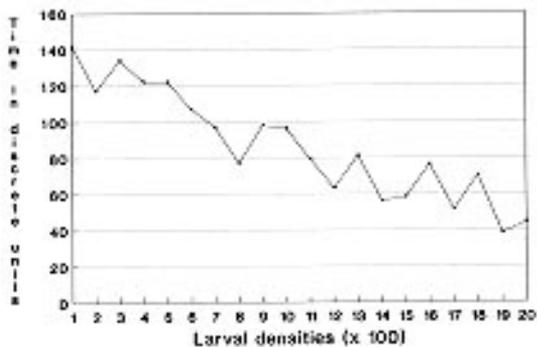
Fig. 4: time in discrete units taken for larvae of *Chrysomya putoria* to exhaust food supply in 20 larval densities.

high levels of competition for food and reproduces the characteristics of exploitative competition encountered in natural populations (de Jong 1976). The number of survivors until pupariation and the values of mean maximum pupal weight obtained for all densities in the experimental setting of the present study, are necessary for the estimation of the amount of consumable food by survivors, obtained through the model developed by Ullyett (1950).

This model considers the effect of density-independent larval mortality to obtain the theoretical value of consumable food, since the density-independent mortality during the density-dependent stage yields a different estimate of composite parameters (Morris 1990), as that obtained by the method of Hassell et al. (1976). The small theoretical value of 0.6% obtained for this parameter in *C. putoria* could be explained by the high levels of competition experienced in the majority of densities performed here, characterizing a pronounced density-dependent effect on survival. This is probably related to the fact that the process of exploitative competition for food reproduced experimentally in this study showed high levels of mortality in the initial larval stage.

The high values of amount of consumable food by the survivors, obtained in the densities 500 to 900, 1,300 and 1,800 larvae are probably due to the high values of probability of acquiring food and number of pupae in these densities. The values in discrete units of time taken for the larvae to attain the minimal pupal weight, are usually larger in the densities where the minimal pupal weight is high, and the proportional difference between minimal and maximum pupal weights is small (which corresponds to higher minimal/maximum pupal weight ratios). Although in these densities the values of probability of acquiring food are usually high, more time in discrete units is necessary for the larvae to attain higher values of minimal pupal weight. The decrease in the values of discrete units

of time needed for the larvae to exhaust the food supply, with increasing larval densities, is indicative of increasing levels of larval crowding and consequently scramble competition for food. It is worth noting that the amount of consumable food, the time needed for the larvae to attain minimal pupal weight, and the time to exhaust food are not monotonic functions of increasing larval densities. This occurs because the calculations of these parameters are based on values of consumable food whose variation also is not monotonic, probably due to variation in the number of pupae and pupal weight in increasing larval densities. The outcome of competition for limited resources in *C. putoria* depends on levels of mortality in the immature stages (Reis et al. 1994), which may be responsible for oscillations mainly in the number and size of pupae formed.

High values of probability of acquiring food per unit of time and consequently small times to exhaust the food supply, as obtained in some larval densities for *C. putoria*, are both indicative of rapid exhaustion of food resources. They also imply situations with high levels of larval competition for food, where all individuals try to acquire as much food as possible in a minimal possible interval of time, as expected from exploitative competition for food (de Jong 1976, Levot et al. 1979, Lomnicki 1988). In this case, the first larvae to attain the minimal weight required for growth and development during larval competition have the highest viability in their developmental trajectory (Denno & Cothran 1976, Hanski 1987).

For larvae whose development occurs in ephemeral substrates, intraspecific competition can have an adverse effect on fitness traits such as survival and size, which has consequences for the population dynamics of the resultant adults (Norris 1965, Kneidel 1984, Goodbrod & Goff 1990). In these substrates, conditions are suitable for rapid development and differences of only a few hours in the hatching time of the larvae may result in marked differences in the size of the larvae at later stages. This may be of major importance, especially in the case of small pieces of carrion, which probably predominate in nature, where resources may be consumed before the smaller larvae reach the size necessary for further development (Hairston et al. 1960, Hanski 1977).

The procedure employed in this study, albeit indirect and utilizing theoretical estimate of ECI, has some advantages over those that rely on physiological or behavioural parameters, in that (1) it makes use of quantities that have a direct bearing on ecological processes such as pupal size and competition, density dependence, and fitness traits such as survival; (2) these data can be easily obtained experimentally and directly employed in measures

of population dynamics; (3) larval density is incorporated as an important variable in the calculations and (4) the method allows for a model evaluation of the theoretical estimates through comparisons with experimental data. In addition, in insects whose immature stages develop inside the food source, the measurement on the amount of food remaining after the larvae have pupated is problematic, because it is difficult to separate faeces from the remaining substrate. So, we believe the procedure outlined here may be applicable to other kinds of insects whose immature stages develop inside the food source, where the estimates of consumable food are difficult to obtain by traditional procedures.

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