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APPLICATION OF WYATT-WHITE METHOD TO CALCULATING INTRINSIC RATES OF INCREASE FOR HYMENOPTEROUS PARASITOIDS

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Abstract The method developed by Wyatt and White (1977) was applied to calculate the intrinsic rates of increase for parasitoids based on 23 fecundity data sets from the literature. The studies showed that there existed the linear relationship between the accurate values of r_m and ln (M_d) / d or ln $(M_{d/2})$ / d, that is, 1) $r_m = 0.845 \ln (M_d) / d$ or 2) $r_m = 0.880 \ln (M_{d/2}) / d$. Where d is the prereproductive time, M_d is the number of female offspring produced per original female from the first to the d^{th} day of reproduction, and $M_{d/2}$ is the number of female offspring produced per original female from the first to the $(d/2)^{th}$ day of reproduction. These equations can provide the accurate estimates of r_m for parasitoids in this study. The approach is advantageous because it does not require the construction of detailed fecundity tables for estimating parasitoid rates of increase. Of course, whether these equations are appropriate for the other taxa will need to be further studied.

Key words: Parasitoid, Intrinsic rate of increase, Calculation

Introduction

The intrinsic rate of increase, r_m, is one of the most important biological parameters of parasitoids against pest insects. In the past, the calculation of r_m values for parasitoids was based on the accurate or the approximate methods of Birch (1948). These methods deal with not only complex calculation, but also detailed information on fecundity. The detailed fecundity tables for parasitoids are often difficult and time-consuming to compile. Therefore, it is necessary to develop a simple method for determining r_m of parasitoids.

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Howe (1953), Laughlin (1965), and Wyatt and White (1977) have all developed methods for calculating r_m, however, the one developed by Wyatt and White (1977) is the most simple. To date, this calculation has only been used for species of aphids and mites and has not been tried for other insects such as parasitoids. Because of the importance of r_m in biocontrol studies, our objective was to expand the method of Wyatt and White (1977) to obtain a simple, yet accurate, method for calculating the r_m value of insect parasitoids.

Methods

Wyatt *et al.* (1977) developed the following equation to calculate the r_m value for aphids and mites:

$$r_m = c \ln (M_d) / d \qquad (1)$$

where d is the prereproductive time from birth to the first day of reproduction, c is a correction constant, and M_d is the effective fecundity calculated by:

$$M_d = \sum_{x=0}^{2d-1} l_x m_x = \sum_{x=0}^{2d-1} f_x / N_0 \qquad (2)$$

In equation 2, x represents age, N_0 is the original number of female, l_x is the age-specific survival rate, m_x is the age-specific fecundity for the mean number of female offspring produced per unit time by a female aged x, and f_x is the number of female offspring produced at age x. In practice, M_d is the number of female offspring produced by each original female in the period 2d. Equation 1 and 2 show that a fecundity table is not needed to calculate the value of r_m because this value is based on the parameters d, f_x and No.

Studies by Wyatt and White (1977) and Gerson (1983) suggested that the best correction constant in equation 1 was ca. 0.74 for aphids and mites. Because of differences in the biology and ecology of aphids and mites compared to parasitoids, we anticipated that a different correction factor would be needed. Thus, in order to determine the most appropriate value of c for parasitoids, we regressed r_m, calculated by the accurate method of Birch (1948), on the factor ln (M_d) / d and ln $(M_{d/2})$ / d, respectively.

The factor ln $(M_{d/2})$ / d was introduced in order to shorten the required time for observing daily fecundity. By reducing the required reproductive period, we could derive the following equation from equation 1:

$$r_m = c' \ln (M_{d/2}) / d \qquad (3)$$

where $M_{d/2}$ is the number of female offspring produced by each original female in d+(d/2) days. This means that equation 2 becomes:

$$M_{d/2} = \sum_{x=0}^{d+d/2-1} l_x m_x = \sum_{x=0}^{d+d/2-1} f_x / N_0 \qquad (4)$$

The degree to which equation 3 and 4 will be appropriate in calculating r_m for parasitoid populations will depend on how parasitoids distribute their reproductive output overtime compared to aphids and mites. Equation 1 was developed based on the observation that 95% of the reproductive output which contributes to r_m could be achieved in about 2d (DeLoach, 1974; Wyatt and White, 1977) .The values of r_m and reproductive contribution to r_m in specific period were calculated by the methods of Birch (1948) . That is,

$$\sum_{x=0}^{\infty} \exp(-r_m X) l_x m_x = 1 \qquad (5)$$

$$r_m = \ln(R_0) / T \qquad (6)$$

$$C_d (\%) = \sum_{x=d}^{2d-1} \{[\exp(-r_m X) l_x m_x] \times 100\%\} \qquad (7)$$

$$C_{d/2} (\%) = \sum_{x=d}^{(d+d/2)-1} \{[\exp(-r_m X) l_x m_x] \times 100\%\} \qquad (8)$$

where r_m is the intrinsic rate of increase; R_0 is the net reproduction rate; T is the mean generation time; C_d is the percentage of reproduction contribution to the r_m from the first reproduction to the d^{th} day; $C_{d/2}$ is the percentage of reproduction contribution to the r_m from the first reproduction to $(d/2)^{th}$ day.

Results

Regression analysis of r_m values calculated by the accurate method of Birch (that is, equation 5) with respect to ln (M_d) / d and ln (M_d/2) / d produced the following equations, respectively:

$$r_m = 0.845 \ln(M_d) / d \qquad (9)$$

$$r_m = 0.880 \ln(M_{d/2}) / d \qquad (10)$$

Correlation coefficients of 0.999 ($p < 0.001$) and 1.000 ($p < 0.001$), respectively, were obtained between each r_m value and thatcalculated by the accurate method of Birch. Thus, the correction constant (c) in equation 1 was 0.845 for r_m calculated with M_d and 0.880 in equation 3 for r_m calculated using the shorter reproductive period $M_{d/2}$.

Based on the fecundity data from the literature, the parameters M_d, $M_{d/2}$, C_d, and $C_{d/2}$ were calculated using equation 2, 4, 7, and 8, respectively (Table 1). The results showed that the reproductive contribution to r_m from the first to the d^{th} day of reproduction is 100% in thirteen cases, > 99% in nine cases, and 95.84% in one case. These results are similar to those obtained by Wyatt and White (1977) and suggested that the distribution of reproduction for parasitoids is the same as that for aphids. It is also apparent that the period from the first to the d^{th} day of reproduction has such a significant effect on the resulting r_m value that any further reproduction can be ignored. Thus, reproduction after 2 d can be considered negligible and R_0 can be substituted by M_d according to equation 2 and let $T = d / c$ in the approximate method of Birch (see equation 6) (Kuang *et al.*, 1992). This will result in the same equation as that developed by Wyatt and White (equation 1). The correction constant (c) in this equation is 0.845 for parasitoids (see equation 9).

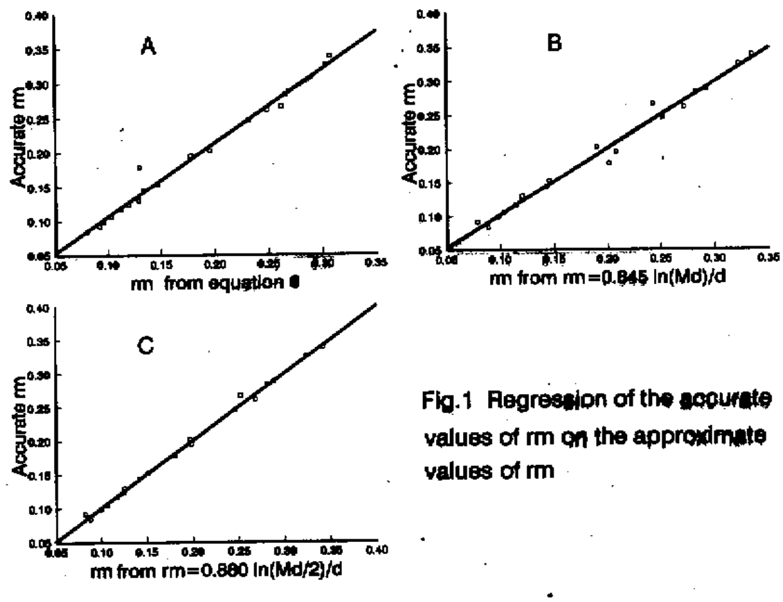

Fig.1 Regression of the accurate values of rm on the approximate values of rm

Similarly, the data in Table 1 showed that reproduction from the first to $(d/2)^{th}$ day of reproduction contributes a large percentage to the r_m values (95% in fourteen cases; > 90% in six cases; and > 82% in three cases). In this case, R_0

Tab. 1 The length of the reproductive period and contribution of different components to the intrinsic rate of increase (r_m) in the reproductive periods of d and d / 2 for 23 fecundity data sets taken from the literature

Species	Temperature (℃)	Prereproductive time (d)	M_d ①	$M_{d/2}$	C_d (%)	$C_{d/2}$ (%)	Source
Goniozus emigratus	26.7	17.0	58.33	32.69	95.84	82.04	Gordh *et al.* (1981)
Muscidifurax zaraptor	—	20.5	157.18	102.85	99.85	91.54	Coats (1976)
Nasonia vitripennis	26.7	14.5	105.79	84.36	100.00	94.36	Nagel *et al.* (1964)
Platygaster californica	20—27	46.0	74.15	74.15	100.00	100.00	Force (1970)
Tetrastichus sp.		27.0	97.75	77.69	100.00	96.89	
Totrymus baccharicidis		38.0	53.91	44.40	100.00	94.86	
Pseudeucoila sp.	25.0	18.5	203.01	202.25	100.00	100.00	Chabora *et al.* (1979)
Praon exsoletum (= *palitans*)							
Sex ratio = 1; Teggs ②	21.0	14.5	255.15	206.92	100.00	96.92	Messenger (1964)
Sex ratio = 1; Eeggs			150.55	116.98	99.96	95.09	
Sex ratio = 0.5; Teggs			127.69	103.46	99.98	95.98	
Sex ratio = 0.5; Eeggs			75.13	58.35	99.93	93.70	
Sex ratio = 1; Teggs	12.5	33.5	123.01	117.83	100.00	99.26	
Sex ratio = 1; Eeggs			95.65	90.93	100.00	99.03	
Sex ratio = 0.5; Teggs			61.48	58.90	100.00	99.08	
Sex ratio = 0.5; Eeggs			47.87	45.51	100.00	98.82	
Trichogramma minutum	25.0	9.0	35.44	32.95	99.95	99.16	Smith (1985)
	20.0	16.0	36.45	36.13	100.00	99.89	
	17.0	21.0	38.08	37.73	100.00	99.93	
	15.0	26.0	41.36	41.22	100.00	99.94	
Ephedrus califonicus							
Sex ratio = 0.66; Teggs	—	13.0	749.17	477.40	99.92	91.44	Mackauer (unpublished)
Sex ratio = 0.66; Eeggs			238.07	135.96	99.39	87.36	(cf. Cohen *et al.*, 1987)
Sex ratio = 0.5; Teggs			567.55	361.66	99.86	90.74	
Sex ratio = 0.5; Eeggs			180.37	103.00	99.29	86.27	

① M_d = the number of female offspring per original female parasitoid over 2d days; $M_{d/2}$ = the number of feamle offspring per original female produced in d+d / 2 days from birth; C_d = the contribution to the intrinsic rate of increase (r_m) between the first and dth days of reproduction; and $C_{d/2}$ = the contribution to r_m between the first and (d / 2)th day of reproduction.

② Teggs = all eggs laid or total fecundity; and Eeggs = the effective fecundity corrected for superparasitism by counting only one egg per host.

will be replaced by $M_{d/2}$ and T will become (d / 2) / c. The similar equation, $r_m = c' \ln (M_{d/2}) / d$ (where c' = 2c), will result. The correction constant (c') in this equation is 0.880 for parasitoids.

When the values of r_m calculated by Birch's accurate method (equation 5) were regressed on those derived from Birch's approximate method (equation 6), and equation 9 and equation 10, without constant item, respectively, the result suggested that equation 9 and equation 10 were more accurate than the approximate equation of Birch (equation 6) in their estimation of r_m with the closest estimate of Birch's accurate r_m being obtained using equation 5 (Fig. 1 a, b and c).

Discussions

1. The estimation of r_m using equation 9 and 10 was based on the linear relationship between the accurate value of r_m by Birch's method and the factor $\ln (M_d) / d$ or $\ln (M_{d/2}) / d$. This is very similar to the cases studied by Wyatt and White. In our cases, correction constants were larger than 0.74, perhaps because parasitoids have longer period of reproduction in comparison with aphids and mites.

2. Equation 9 and 10 can provide the accurate estimate of r_m for all data in this study. This seems to show that the method developed by Wyatt and White can be applied to the estimation of r_m for parasitoids or the other with the minor changes of correction constant (c).

3. On the other hand, equation 9 and 10 do not require the fecundity tables when they are used in calculating r_m values. When the parameters d, M_d or $M_{d/2}$ are known, the r_m can be estimated.

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应用 Wyatt–White 方法计算寄生物种群 r_m 的研究

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摘要　本文是关于应用 Wyatt–White 方法计算寄生物种群内禀增长率的研究。研究表明：r_m 的精确值与 ln (M_d) / d 或 ln ($M_{d/2}$) / d 之间存在着线性关系，这种关系可表达如下：(1) $r_m = 0.845 \ln (M_d) / d$；(2) $r_m = 0.880 \ln (M_{d/2}) / d$。这里 d 为生殖前期；$M_d$ 为生殖起初 d 天内每个原始雌虫产下的平均雌性后代数；$M_{d/2}$ 为生殖起初 d / 2 天内每个原始雌虫产下的平均雌性后代数。运用 23 组生殖力表资料，研究表明公式 1—2 可以给出 r_m 的精确估计值，公式 2 的估计效果更好。这种方法不要求组建生殖力表。该方法是否适用于其它寄生物种群或其它生物类群有待进一步研究。

关键词：寄生物，内禀增长率，计算