ESTIMATION OF MORTALITY OF *CHORTOICETES TERMINIFERA* (WALKER) (ORTHOPTERA: ACRIDIDAE) FROM PARASITISM BY *BLAESOXIPHA RUFIPES* (MACQUART) (DIPTERA: SARCOPHAGIDAE)

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Summary

A method is given for correcting field determined rates of apparent parasitism for sampling inefficiency and a formula given to estimate the mortality of a host generation which takes into account parasite turnover during the susceptible stage of the host.

Introduction

Estimation of the reduction in productivity of grasshopper and locust populations as a result of mortality caused by parasitoids is notoriously difficult (Joern and Gaines 1990). Some difficulties are specific to studies on insects such as locusts, because of their behaviour patterns. For example, estimates of changes in the density of the host population are affected by the migratory behaviour of locusts and the density compensating effects of their gregarious behaviour in declining populations. Other difficulties arise from sampling inefficiencies, either at the time of assessment or caused by the frequency of sampling (Van Driesche *et al.* 1991, Onsager 1993).

The level of apparent parasitism (P_a) by *Blaesoxipha rufipes* (Macquart) (= *pachytyli* (Skuse) (Pape 1994)), determined by field dissection (Baker and Pigott 1995), cannot be directly equated with mortality caused by parasitism (M) for two reasons. Firstly, P_a may need to be corrected for small larvae or larvae in torpid hosts (P_c). Secondly, mortality rate can only be equated with P_c if there is only one generation of parasitoid during each generation of the host. Generation time of *B. rufipes* is much less than that of *Chortoicetes terminifera* (Walker), so calculation of mortality must take into account parasite turnover.

This study addresses these difficulties in relation to *B. rufipes* when parasitising *C. terminifera*, by attempting to quantify the relationship between apparent parasitism and host mortality. The terminology used for parasitoid growth stages and the development times of *B. rufipes* are from Baker (1995: as *B. pachytyli*).

Results and Discussion

Estimation of Corrected Parasitism (Pc)

The level of apparent parasitism (P_a) for *B. rufipes* determined by field dissection is the percent of sampled locusts in which parasitoids are detected. P_a systematically underestimates the real percent of parasitised locusts (P_c) due to: (a) failure to detect early first instar larvae in the lag period of development and (b) failure to sample torpid or moribund hosts harbouring replete larvae.

The total development time (TDT) of developing *B. rufipes* larvae can be conveniently divided into the growth phases defined by Levot *et al.* (1979): a lag phrase (LP), followed by a period of most rapid growth (PMRG), and finally a stationary phase (SP). The LP and the PMRG together comprise the mean larval development time (MDT).

During the LP, the larvae are too small to be observed by field dissection. A simple correction factor can be calculated by assuming that the proportion of undetected larvae is constant, that there is a relatively constant rate of larviposition, and that the proportion of the total larvae which are in any given stage of development is equal to the duration of that stage expressed as a proportion of the MDT:

$$\frac{P_a}{P_c} = \frac{(MDT - LP)}{MDT}$$

or EQUATION 1

$$P_c = \frac{P_a}{1 - \frac{LP}{MDT}}$$

where P_c is % parasitism corrected for LP larvae; P_a, % apparent parasitism; LP, mean duration of lag period of growth of first instar; MDT, mean larval development time of *B. rufipes*.

Correction for failure to sample torpid hosts, parasitised by replete larvae in the SP, is not required if MDT is used in preference to TDT. Calculation of host mortality is not affected provided MDT is used in subsequent calculations of parasite turnover. However, if correction is required for both LP and SP, the corresponding equation is:

EQUATION 2

$$P_{ct} = \frac{P_a}{1 - \frac{SP}{TDT} - \frac{LP}{TDT}}$$

where P_{ct} is % parasitism corrected for LP and SP larvae; TDT is mean total development time of parasitoid; SP, stationary period of third instar larvae.

If this estimate is used, P_{ct} and TDT should be substituted for P_c and MDT respectively in Equation 3 and the following discussion.

Correction may be required for SP only, for example for locusts collected from the field but dissected in the laboratory, where first instar larvae are readily detected. In this case, P_{cs} can be calculated by substituting SP/TDT for LP/MDT in Equation 1, and P_{cs} should be substituted for P_c in Equation 3 and the following discussion.

Values of LP, SP, MDT and TDT for *B. rufipes* larvae developing in several stages of *C. terminifera* at a range of constant temperatures are given in Baker (1995).

The relative duration of the stages of larval development are independent of temperature (Baker 1995) and it is therefore not necessary to consider the ambient temperature in the field when estimating P_c. The relative duration of the stages is, however, influenced by host stage (Baker 1995). The mean value of the ratio LP/MDT in adult hosts is 0.48 and in nymphs 0.54 (Baker 1995).

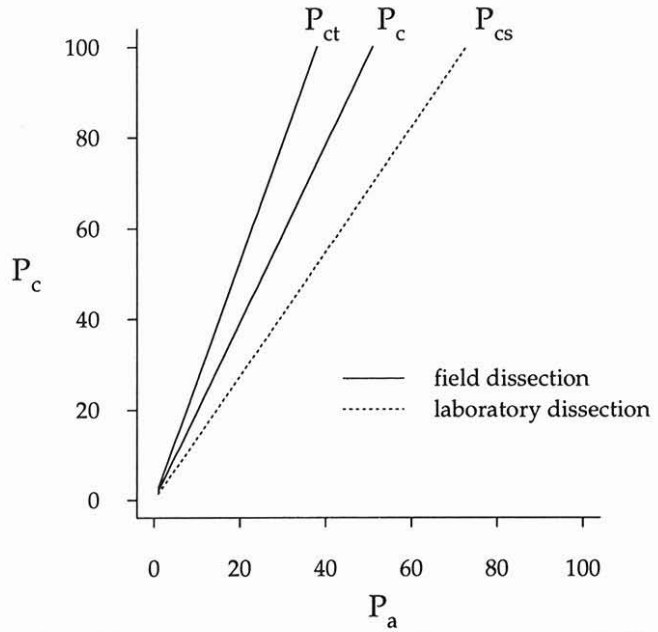

Fig 1. Corrected parasitism (P_c) in relation to apparent parasitism (P_a) taking account of differences in search efficiency for field and laboratory dissection of the host *Chortoicetes terminifera*: P_c, corrected for lag period of first instar larvae (equation 1); P_{cs}, corrected for stationary period of growth of third instar larvae; P_{ct}, corrected for both lag and stationary periods (equation 2).

The relationships between P_c, P_{ct}, P_{cs} and P_a are shown in Figure 1.

Estimation of host mortality

Once an estimate of P_c has been obtained, an estimate of host mortality (M) resulting from parasitism over a particular period of time (T) is required. The time period may be, for example, an entire host stage, or the intervals between sampling. Since the duration of the parasitic stage of *B. rufipes* is much less than the duration of the susceptible stage of *C. terminifera*, it is necessary to take parasite turnover during T into account when estimating M.

The change in the number of hosts as a result of parasitism, ΔN, during a short time period, Δt, can be estimated as the number of parasitised hosts multiplied by Δt expressed as a proportion of the total time for host to die. If Equation 1 is used to estimate P_c, then the time for the host to die is taken as MDT; if equation 2 is used, then TDT should be substituted for MDT in Equations 3 to 5. P_c is assumed to be constant during the time period being considered. Then:

EQUATION 3

$$\Delta N = -\frac{\Delta t}{MDT} \times \frac{P_c}{100} \times N$$

where ΔN is the change in the number of hosts due to parasitism during time Δt and N is the total number of hosts at the beginning of Δt.

Equation 3 can be divided throughout by N, and the expression integrated from time 0 to time T to estimate N_T, the number of hosts alive at time T. If T = MDT, then the number of hosts dying during T as a result of parasitism can be estimated as the number parasitised initially at time 0. Hence:

EQUATION 4

$$\log_e(N_T) = \frac{P_c}{100} \times (1 - \frac{T}{n}) + \log_e(N_0(1 - P\frac{c}{100}))$$

where N_0 and N_T are the number of hosts at time 0 and T respectively.

Since :

$$M = \frac{N_0 - N_T}{N_0} \times 100$$

M can be estimated as:

EQUATION 5

$$M = (1 - (1 - P_c) \times \exp(P_c) \times \exp(-\frac{T}{MDT} \times \frac{P_c}{100})) \times 100$$

where M is per cent host mortality caused by parasitism for time period T.

Equation 5 assumes constant P_c during T. However, substantial increases in parasitism level, possibly 4-5 fold, may occur between generations of the parasitoid. The greater the value of T, the less accurate the assumption of constant P_c will be. There are also seasonal differences in activity of *B. rufipes*. In late spring and early summer, *B. rufipes* activity is highly synchronised and of short duration relative to the duration of the host stage, due to the synchronising influence of overwintering pre-pupal diapause. During late summer and autumn, activity is unsynchronised and of longer duration relative to the duration of the host stage. Ideally, sampling intervals should be chosen

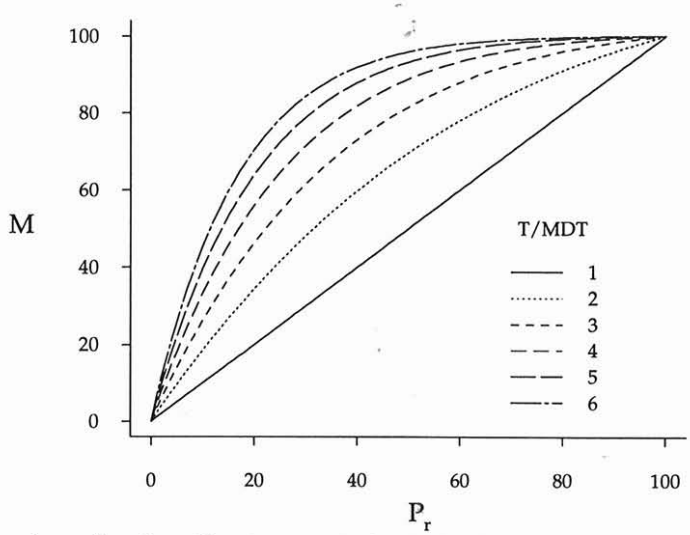

Fig 2. Estimated mortality of host *Chortoicetes terminifera* (M) in relation to corrected parasitism rate (P_c) for *Blaesoxipha rufipes* for a range of values of T/MDT.

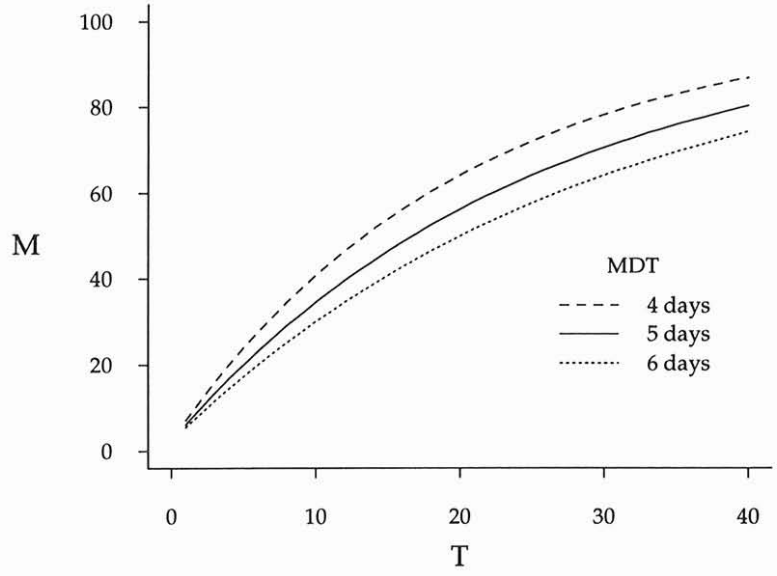

Fig 3. Estimated mortality of host *Chortoicetes terminifera* (M) in relation to duration of host stage (T), in days, for three values of mean development time (MDT) of *Blaesoxipha rufipes* larvae, for a host population with a sustained corrected parasitism rate (P_c) of 20%.

which take seasonal differences in P_a into account. Equation 5 also assumes mortality of all hosts following emergence of replete larvae.

Figures 2 and 3 show M estimated using Equation 5 for varying values of P_c , T and MDT . Figure 2 shows the increase in estimated M caused by increasing T/MDT from 1 to 6. For example, for P_c = 10%, 2 periods of parasite turnover would cause an estimated mortality of 19%; 6 periods would increase estimated mortality to 45%. Figure 3 shows the effect of varying mean development times on the estimate of M for a sustained P_c of 20%. For example, over a period of 40 days, an increase in MDT from 4 to 6 days decreases estimated mortality by 12%.

If more than one sample is taken during a host stage, the mortality of the stage can be calculated from the mortality calculated for each sample:

EQUATION 6

$$M_s = \left(1-\left(\left(1-\frac{M_1}{100}\right) \times \left(1-\frac{M_2}{100}\right)\ldots\right) \times 100\right.$$

where M_1, M_2 are mortalities during sampling intervals 1, 2 etc.

Mortality of host generation

The mortality of a host generation (hoppers and adults) can be calculated using the equation:

EQUATION 7

$$M_g = \left(1-\left(1-\frac{M_{s1}}{100}\right) \times \left(1-\frac{M_{s2}}{100}\right)\right) \times 100$$

where M_g is the per cent mortality of the host generation; M_{s1}, mortality of first stage (nymphs); M_{s2}, mortality of second stage (adults).

The effect of mortality on reproductive rate

The contribution made by *B. rufipes* to the natural mortality of the post-embryonic stages of the host may be substantial and in general terms there is a proportional reduction of the potential reproductive rate (Farrow 1979, Southwood 1966). The resulting reproductive rate can be calculated by the equation:

EQUATION 8

$$R_0 = PR_0 \times (1 - \frac{M_g}{100})$$

where R_o is the reproductive rate, depressed as a consequence of mortality;
PR_o potential reproductive rate of host species.

Mortality of adults after the onset of egg laying does not result in a proportional reduction in the reproductive rate, as some of those parasitised have already played a role as effective parents of the next generation. This shortcoming can be rectified by an arbitrary truncation of the value of T for the adult stage to the pre-oviposition period of the host in the calculation of M_{s2}. Sanchez and Onsager (1994) have reported effects of dipterous parasitoids, including *B. reversa* (Aldrich) and *B. hunteri* (Hough), on reproduction of *Melanoplus sanguinipes* sampled from the field.

Equation 8 fails to take into account the small sexual bias in the levels of apparent parasitism in favour of female hosts. It is therefore more appropriate to base calculation of the depression of the reproductive rate on data for female hosts rather than populations.

TABLE 1

Seasonal variation in mortality of generations of *Chortoicetes terminifera* based on typical levels† of apparent parasitism recorded for *Blaesoxipha rufipes*.

Host		Parasitism			Parasitoid turnover		Host mortality	
Generation	Stage	P_a %	LP / MDT	P_c %	T days	MDT days	M_s %	M_g %
Spring	nymph	0.3	.54	0.65	73	5.8	7.9	
	adult	0.9	.49	1.76	54	5.6	15.6	22.3
Summer	nymph	1.7	.54	3.70	64	4.6	40.3	
	adult	4.2	.49	8.24	50	4.3	61.8	77.2
Autumn	nymph	4.0	.54	8.70	66	5.8	63.0	
	adult	9.0	.49	17.65	36	5.6	68.4	
	adult *	18.0	.49	35.29	20	5.6	73.9	97.0

P_a = apparent rate of parasitism; LP = duration of 1st larval instar (from Baker 1995); MDT = mean larval development time (from Baker 1995); P_c = corrected rate of parasitism; T = duration of host stage (from Farrow 1977); M_s = mortality of host stage; M_g = mortality of host generation

* resdiual autumn generation, with higher parasitism rate

† recorded during outbreaks on North West Slopes and Plains of N.S.W. 1979, 1991 (Baker and Pigott unpublished data)

Example of host mortality estimated from mean levels of apparent parasitism

An example of the calculation of stage specific host mortality from apparent parasitism based on data from the North-West Slopes during the 1979 and 1991 outbreaks of *C. terminifera* (Baker and Pigott unpubl. data) is given in Table 1.

The levels given for P_a are typical values recorded for the two outbreaks. In both years, there was a substantial increase in parasitism during the season. In Spring, parasitism was low, and typically highly variable. However, even the very low levels of early Spring can be seen to cause significant mortality. In autumn there was high, relatively constant parasitism, which was a major cause of host mortality.

The magnitude of the discrepancy between P_a and M_g confirms the need to take into account the difference in the relative duration of the parasitic stage of *B. rufipes* and the susceptible stage of the host *C. terminifera* when assessing the impact of this parasitoid on mortality of the host.

General

The literature contains numerous examples where a single estimate of apparent parasitism by *B. rufipes* (as *pachytyli*) has been equated with the mortality of the host generation (Olliff 1891, Froggatt 1901, 1910, Gurney 1908, Noble 1936, Weddel 1937). Also, erroneous comparisons of the roles played by different species of parasitoid have resulted from failure to take into account the relative duration of their parasitic development. These assessments of the relative importance of specific parasitoids and their role in the population dynamics of locusts and grasshoppers have persisted, despite the false premise on which they were based. In this paper, we have shown how great the discrepancy between apparent parasitism and mortality can be, and that assessments of the effect of locust parasitoids on host populations, particularly the effect of *B. rufipes* on the population dynamics of *C. terminifera*, must take parasite turnover into account.

Acknowledgments

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