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Data Collection and Analysis in a Continuing Study of
the Swaine Jack Pine Sawfly Life System¹

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Some natural populations show surprisingly stable periodic increases and decreases. The lemming cycle in the arctic (Lack, 1954) and the familiar lynx-hare oscillations (Kormondy, 1969) are among the most spectacular, as are also the fluctuations of the larch budmoth (Baltensweiler, 1970) which have exhibited an amplitude of five orders of magnitude and a regular 7-year period over the last several decades. Various explanations have been proposed for the oscillations (Odum, 1970), and cyclic populations continue to attract serious attention from ecologists, since they are usually observed in less complex ecosystems, thus facilitating study. The oscillations may reflect regulating mechanisms common to all systems, but less apparent in the more complex ones.

There is a body of theoretical ecology, largely based on the pioneering work of Nicholson and Bailey (1935), based on a number of fundamental assumptions, among which are: in order to exist and produce offspring, animals must obtain food, mates, and a suitable place to live; searching by populations is always random; populations are self-governing systems; the mechanism of regulation is almost always intraspecific competition, either amongst the animals for a critically important requisite, or amongst natural enemies, for which the animals concerned are requisites. A short review of the development of competition theory is now given to facilitate discussion of data collection and analysis, and the development of a simple host-parasitoid model in a continuing study of the Swaine jack pine sawfly Neodiprion swainei Middleton, which appears to have some of the properties of an oscillating species.

The basic Nicholson-Bailey host parasitoid model is as follows: assume the host insect has a unique steady density HN ; the parasitoid its own steady density, PN ; the parasitoid searches at random and has a specific area of search, A ; the power of increase of the host, F , is fixed, and time is defined in generations as $I = 1, 2, \dots, N$, then:

$$\begin{aligned} I &= 1 \\ HN_{I+1} &= HN_I \times e^{-A \times PN_I} \\ PN_{I+1} &= HN_I - HN_{I+1} \\ HN_{I+1} &= HN_{I+1} \times F \\ I &= I + 1 \end{aligned} \tag{1}$$

¹ Based in part on a talk delivered at the Annual Meeting of the Northeastern Forest Insect Work Conference, Pennsylvania State University, March 20-22, 1974.

If populations of hosts and parasitoids are explored over N generations it is seen that hosts and parasitoids oscillate, the parasitoid oscillation lagging behind that of the host, and the oscillations increase dramatically in amplitude until either the host or the parasitoid is driven to extinction. Such models are unrealistic since most ecological systems are stable for extended periods, i.e. populations may oscillate either regularly or irregularly but persist for fairly long periods of time without elements of the system being driven to extinction.

A major refinement of the model, in which the basic distribution of the attacks of the parasitoid are described by a negative binomial distribution, was first proposed by Griffiths and Holling (1969). The negative binomial distribution, developed by Fisher (1953) describes the distribution of a wide variety of organisms in nature. The distribution is defined by its two parameters, the arithmetic mean, m , and an exponent, k , which is a measure of the degree of contagion in the distribution. Its basic form is $(q - p)^{-k}$, and the proportion of individuals in the 0 category of the distribution is, by expansion, $P_0 = 1/q^k$ where $p = m/k$ and $q = 1 + p$. The value of the exponent k may be found by maximum likelihood from the expression

$$N_0 = 1/(1 + m/k)^{-k}$$

where N_0 is the number of 0 counts in the distribution (Waters and Henson, 1959). If the attacks of the parasitoid are described by a negative binomial distribution with an exponent, k , and a mean, m , the recursion becomes:

$$\begin{aligned} I &= 1 \\ HN_{I+1} &= HN_I \times (1 + (A \times PN_I/k))^{-K} \\ PN_{I+1} &= HN_I - HN_{I+1} \\ HN_{I+1} &= F \times HN_{I+1} \\ I &= I + 1 \end{aligned} \tag{2}$$

Concerning Nicholson and Bailey's original assumptions, nothing is changed. The search of parasitoids is still random (unorganized). The distribution of attacks of the parasitoid, however, is contagious. The exponent k , in the distribution ranges from 0 to ∞ . As k approaches ∞ the distribution converges to the Poisson and the model then becomes identical to (1). Therefore, the Nicholson-Bailey model is a limiting case of the general model where the distribution of attacks of the parasitoid are described by the negative binomial distribution (Griffiths and Holling, op. cit.).

This means that, as the value of k drops, a greater proportion of hosts escape parasitism at the higher parasitoid/host ratios; in other words, the host has a refuge which tends to counteract the global instability

resulting from the one generation lag in the parasitoid's response. The model therefore seems more realistic than (1) but both suffer in that the number of attacks generated is a linear function of the number of parasitoids searching. This is known not to be true (Holling, 1959) so additional realism may be injected into the model by assuming that the number of attacks generated is described by a Holling Type II functional response, the formula for which is:

$$NA = PN_I \times (TC \times A \times HN_I / 1 + A \times TH \times HN_I) \quad (3)$$

where NA is the number of attacks of the parasitoid, TC = the time the host is available to the parasitoid, TH = the handling time of the parasitoid, and the other parameters are as previously defined. The recursion now becomes:

$$I = 1 \quad (4)$$

If $I = 1$, go to L2

$$L1: NA = PN_I \times (TC \times A \times HN_I / 1 + A \times TH \times HN_I)$$

$$PN_I = NA$$

$$L2: HN_{I+1} = HN_I \times (1 + (A \times PN_I / K))^{-k}$$

$$PN_{I+1} = HN_{I+1} - HN_I + 1$$

$$HN_{I+1} = F \times HN_{I+1}$$

$$I = I + 1$$

If $I \leq (N - 1)$, go to L1

where N = the number of recursions (generations). Note that the number of attacks is fixed at the beginning of the recursion, hence the loop to bypass NA at $I = 1$.

The properties of the model may now be explored most clearly through phase diagrams, where population y (the parasitoid) is plotted as a function of population x (hosts) for year $I = 1, 2, \dots, N$ (Fig. 1). Below $K = 1$, the model is globally stable, but always at the expense of increasing steady densities of both host and parasitoid, so that at $K = 0$, the densities are infinitely high. Only at $K = 1$ is a stable node reached where the populations will continue to oscillate indefinitely with the same amplitude and periodicity. At values of $K > 1$, the model is globally unstable. Clearly, such a model is also unrealistic, since global stability or instability do not seem to characterize natural systems (Holling, 1972). What is needed is an expression which will stabilize the system at values of $K > 1$,

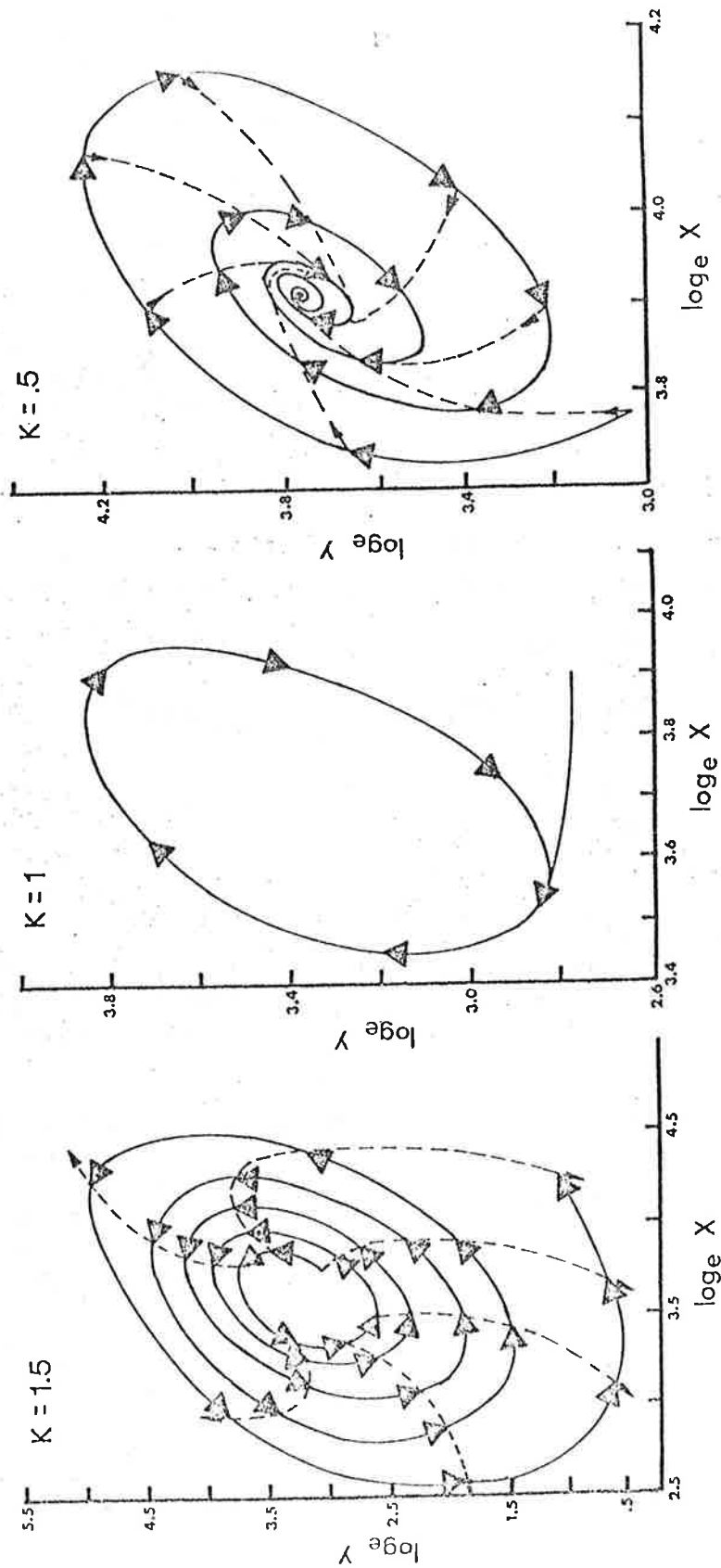


Fig. 1. Phase diagrams showing the output of model (4) (see text) in which the attacks of the parasitoid are described by a negative binomial distribution, and the functional response of the parasitoid is included. Parameters are from Nicholson and Baileys (1935) original example, where $HN = 44$, $PN = 20$, $A = .035$, $F = 2$, and where TC and TH are arbitrarily set at 1 and .005. Output is for $K > 1$, $K = 1$, $K < 1$.

and destabilize it at value of $K < 1$, in other words to produce a stable limit cycle (May, 1972). In the absence of its only regulating agent, the parasitoid, host numbers will increase exponentially and plateau at the replacement level of the resource. This is described by the familiar logistic function:

$$HN_{I+1} = HN_I \times R \times (1 - (HN_I/KK)) \quad (5)$$

where R is the intrinsic rate of increase of the host in the absence of the parasitoid, and KK is the maximum population size attainable. Since it approaches realism, it may be useful to explore the consequences of applying it to a real world situation. It will be expected that populations of the system will oscillate, and populations of the parasitoid will lag behind that of the host. The oscillations will be a property of the population itself and will be relatively independent of extraneous environmental influences. The distribution of attacks of the parasitoid should be described by a negative binomial distribution with an exponent K which is a constant. There will be a defined upper limit beyond which the host will not be able to exist owing to depletion of its requisites, and this level will be above that of the upper level of the host-parasitoid oscillation. Finally, if the parameters of the model (Tables 1, 2) are known, it should, if realistic produce the same periods and amplitudes which characterize the observed host-parasitoid oscillation.

I will now describe data collection and analysis in a continuing study for the Swaine jack pine sawfly life system with particular reference to hosts and larval parasitoids. One of the tasks at the initiation of the study was to construct and analyse life tables for the sawfly and its natural enemies with a view to the development of predictive mathematical models eventually to be integrated into a program of management for jack pine in Quebec. Since the larval parasitoids occupy such an important place in the sawfly's cycle, we have developed life tables for the parasitoids with a view to evaluating their effectiveness.

The Swaine jack pine sawfly is a univoltine diprionid specific to jack pine and is a dominant insect of Quebec jack pine forests. During their lifetime, these sawflies are exposed to the actions of several groups of natural enemies, and the larval parasitoid guild (Root, 1968) is one of the most important. It is composed of five species of which the dipterous Spathimeigenia aurifrons Curran is dominant, comprising over 75 percent of the guild. The remaining are, in order of abundance, the ichneumonids, Olesicampe lophryi (Riley), Lamachus, spp., and the chalcid, Perilampus hyalinus Say; these are all primary parasitoids. The only hyperparasitoid in the guild is the ichneumonid, Euceros frigidus Cress. Their behaviour and emergence patterns have been studied by Tripp (1960, 1961, 1962a, b) and Price and Tripp (1972). They all attack young larvae and pass the winter in the host as eggs or first instar larvae. They resume development in the host in late spring and emerge in time to attack the succeeding generation of sawflies. All are solitary internal parasitoids and do not discriminate against previously deposited progeny, either of their own or other

Table 1. Life table data used in Neodiprion swainei host-larval parasitoid exploitation model.
Obtained from four study areas for an 11 year period, 1962-1972.

Host Stage	Number of Insects/Sq.M.				Survival Rates	
	Unparasitised Sawflies	Parasitised Sawflies	Parasitoid Stage	Total Sawflies (SU)	Unparasitised Sawflies (SULIV)	Parasites (SUPARAS)
Egg	102.9328	-	-	.94384	.94384	-
I Instar	97.1527	-	-	.47958	.47958	-
Larvae before parasitoid attack	46.5931	-	-	.48184	-	-
Larvae after parasitoid attack	31.8231	14.7700	I instar - egg	-	.49594	.45145
Pre-spinning eonymph	15.7825	6.6680	I instar - egg	.76892	.78518	.72894
Cocoon (fall)	12.4021	4.8605	I instar - egg	.57604	.59801	.51997
Cocoon (spring)	7.4167	2.5278	I instar - egg	.36792	.45127	.12332
Emerged adults	3.3469	.31168	adult	.66267	.72438	.50000
Surviving adults	2.4245	.15584	female	.66246	.66246	-
Surviving females	1.6061	-	-	.78948	.78948	-
Adjustment for fecundity	1.2680	-	-	-	-	-

Table 2. Parameters used in Neodiprion swainei host larval parasitoid competition model. Obtained from life table data as in Table 1.

<u>Explanation</u>	<u>Symbol</u>	<u>Value</u>
Initial host density (Eggs/M ²)	HN ₁	1.02932E2
Mean number of larval parasitoid attacks/host	PAR	5.03320E-1
Proportion of emerged parasitoid adults to total emerged insects	PAD	8.51920E-2
Exponent K of negative binomial	K	2.07503E 0
Potential fecundity of sawfly	F	8.11800E 1
Intrinsic rate of increase of host in absence of parasitoid	R	1.464128E-0
Time host available to parasitoid	TC	1
Handling time of parasitoid	TH	1.77400E-3
Upper limit of host density	KK	600

species. Thus, they are typical "scramblers" (Nicholson and Bailey, op. cit.). The mean number of attacks by the larval parasitoid guild averages half the available hosts, and survivorship records (Table 1) show that over 98 percent of the parasitoids die while they are still in the hosts.

It is a somewhat formidable task to collect population data throughout at least one complete oscillation of a host parasitoid system, since several years may be required to completion. Nevertheless, it is necessary, since only then can the life table data be used to test competition theory, since oscillations are implicit in any competition model. It is therefore of fundamental importance to develop a system to provide access to the data base of the life table study, especially since the period of observations may very well exceed the time a scientist or group of scientists are assigned the problem, and allowance must be made for continuous analysis, updating, and access by other workers.

At the base of the data collection system are two manuals, the first coded sampling forms (McLeod, 1973a) which in addition to providing a key to the data base of the project also provide a record of all the variables that are measured in the life system. The second, a sampling manual, in preparation, will provide a reference to all field and laboratory sampling techniques. Host numbers are estimated by techniques developed by Lyons (1964). Parasitoid numbers are estimated through dissection of hosts, since they are all internal parasitoids. They are also present in the host for almost throughout their life so parasitoid population estimates are obtained through dissection of hosts from each collection interval, four in all. Five hundred hosts, when present, are dissected during each collection. These are done in lots of about 60 per day by placing hosts individually in Syracuse watch glasses in a 10 percent solution of KOH overnight to clear the contents of the host so that the parasitoids mouthparts may be observed and identified to species according to techniques outlined by Finlayson (1960, 1963).

It is extremely important, so as not to lose information, that the sampling unit be the individual parasitoid larva. Therefore, all the information pertinent to one parasitoid larva is entered on one sampling form (McLeod, 1973a). From this, frequency distributions of attacks of each parasitoid species as well as species groups, may be compiled. This is essential for the calculation of K of the negative binomial for each species. From these distributions, the number of parasitoid attacks as well as the number of hosts attacked may be recorded. As well, the fate of each individual parasitoid is recorded, and from this, life tables for the parasitoids may be drawn up. Although it is presently impossible to measure variation in adult parasitoid density, the mean density of emerging parasitoid adults may be obtained from dissections of cocoons accumulated in the soil over a period of years (McLeod, 1971).

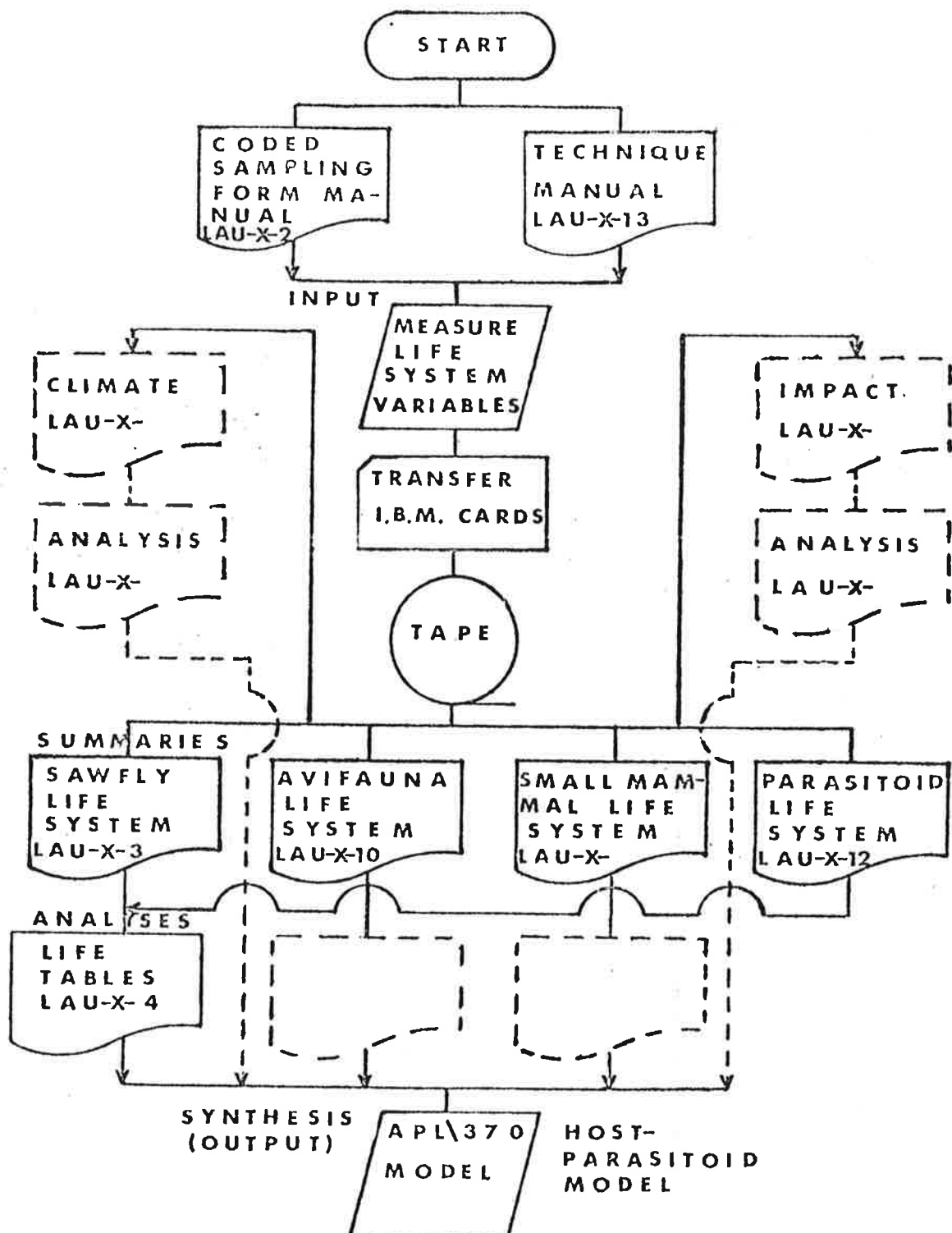


Fig. 2. Flow chart showing data collection and analysis for the Swaine jack pine sawfly life system. Numbers are shown beside manuals completed or in advanced preparation. Others are planned (dotted outlines). The output is a series of mathematical models.

Once the information is compiled on the forms, it is transferred directly to FORTRAN cards and summaries and analyses provided through a series of FORTRAN IV programs (McLeod and Brochu, 1973b). Finally, life tables are developed and analysed (McLeod and Lagu, 1973c). Also under development is a series of manuals providing complete access to analyses of the whole life system (Fig. 2). These will provide public accessibility which is fundamental to scientific method, and will permit reevaluation and further analyses of the data in the light of new theory or analytical techniques.

The sets of measurements required for a test of a simple host-parasitoid model just described are as follows:

1. The number of host eggs per unit area.
2. The numbers of the attacked host stage per unit area.
3. The mean number of attacks per host of the parasitoids.
4. The exponent, K, of the negative binomial distribution describing the attacks.
5. The survival rate of the attacked population.
6. The survival rate of the unattacked population.
7. The potential fecundity of the host.
8. The number of host adult females per unit area.
9. The number of parasitoid adult females per unit area.
10. The effective searching area of the parasitoid.
11. The handling time of the parasitoid.
12. The time hosts are exposed to the parasitoid.
13. The rate of increase of the host in the absence of the parasitoid.
14. The host population level at which resource replacement just balances depletion without loss of quality of the resource.

All except items 10 and 11 may be obtained directly through accumulation of life table data for the host and parasitoid through a complete population oscillation so the parameters then are averages for the system. Ideally, items 10 and 11 should be obtained experimentally; however, if a full oscillation has been measured, the parasitoids area of search may be obtained from the following formula (Nicholson and Bailey, 1935):

$$A = (1/PA_I) \times (\log_e (HN_I/PN_I)) \quad (6)$$

where PA is the parasitoid adult density, HN is the density of hosts prior to attack, and PN is the density of hosts following attack. Following this, handling time may be found by approximation from the functional response formula (3).

A flow chart (Fig. 3) shows the steps in the development of a competition model using the information listed above. First, the vectors for the model's output are dimensioned; these include host density, parasitoid progeny density and parasitoid adult density for 32 generations. The parameters of the model (Table 2) are then set, as are the survival rates for the parasitised and unparasitised hosts (Table 1). The model then starts out with the identity:

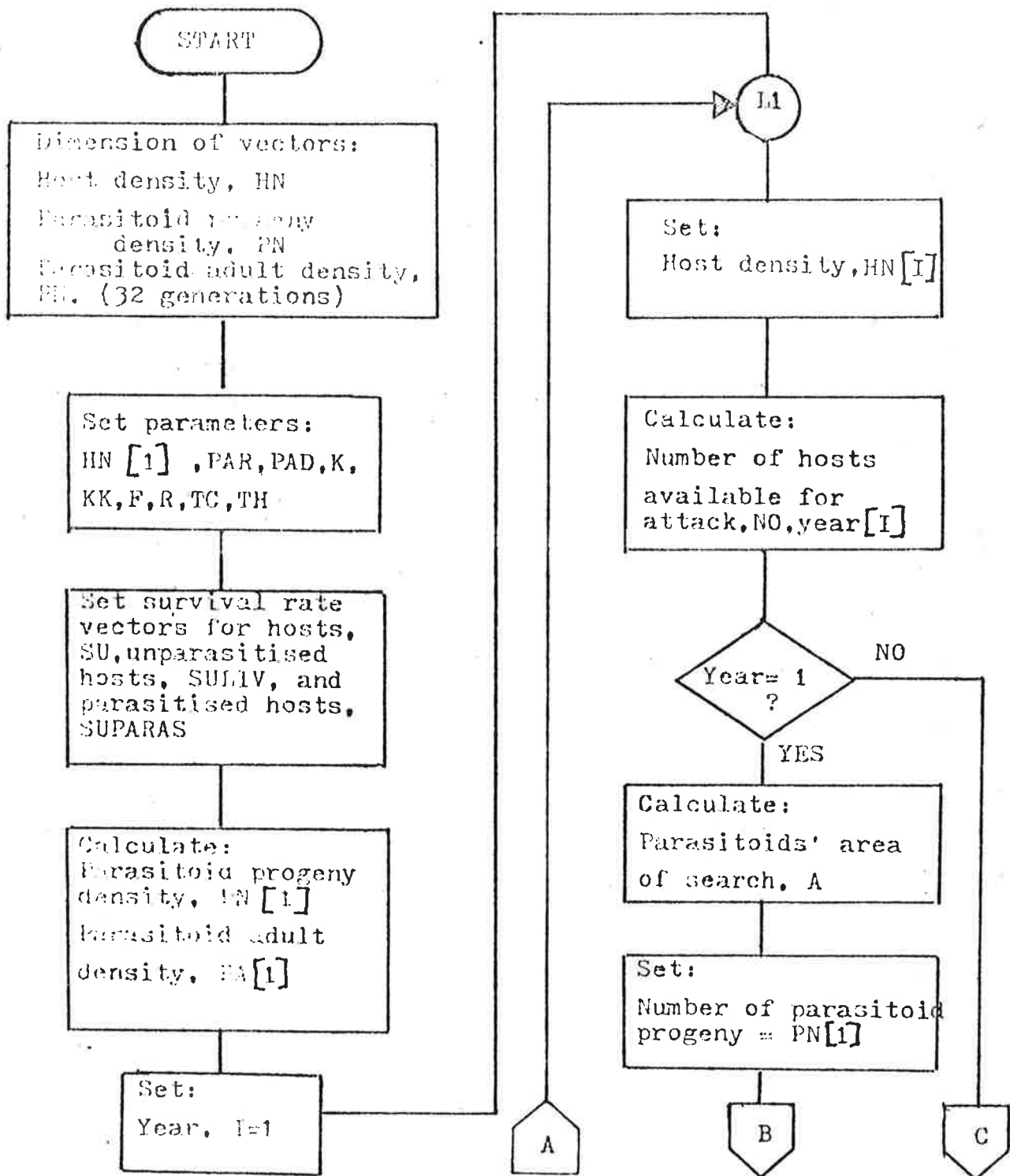


Fig. 3. Flowchart for a host-larval parasitoid model of Swaine jack pine sawfly life system.

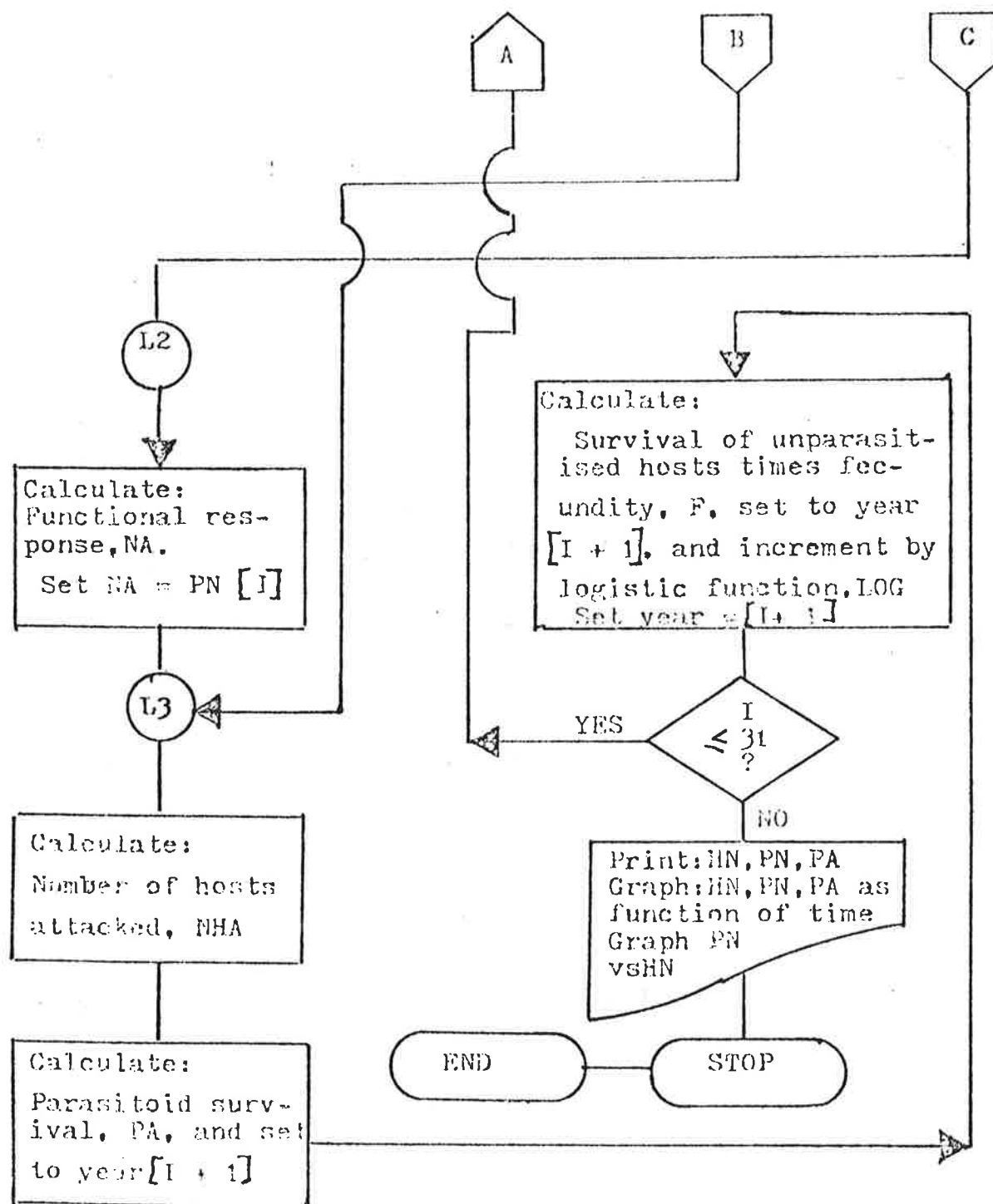


Fig. 3. Flowchart for a host-larval parasitoid model of Swaine jack pine sawfly life system (Cont'd).

$$HN_I = HN_I \times (SULIV_1 \times SULIV_2 \times \dots \times SULIV_{10}) \times F$$

This is a static model with no regulation. Displacement of any of the survival rates in SULIV or of F from their appointed values will drive the system into extinction. Note that mean generation survival of the host was .00419 lower than shown (Table 1) and this was added to each survival to yield a static system. At the measured rates, populations would have doubled in about fifty years.

Parasitoid progeny density, and parasitoid adult density for year 1 are then calculated as follows:

$$PN_1 = HN_1 \times (SU_1 \times SU_2) \times PAR$$

$$PA_1 = HN_1 \times ((SU_1 \times SU_2 \times \dots \times SU_6) \times PAD)/2$$

The year is then set at $I = 1$ and the recursion commences. Host density, HN is set, following which the number of hosts available for attack is calculated:

$$NO = HN_I \times (SU_1 \times SU_2)$$

The parasitoid's area of search is calculated from (6) and the number of parasitoid progeny is set at PN_1 .

If year > 1 , the number of parasitoid progeny, NA is calculated from the functional response (3). The number of hosts attacked is then calculated by (2).

Since there might be some question in assuming the value of K to be constant through a complete population oscillation, we will now consider in some detail the derivation of the parameter. The number of attacks of the larval parasitoids per hosts oscillates strongly (Fig. 4) with a period of 11 years from a low of .05 per host to a high of 1.2 per host, and within this range any change in K as a function of density should be manifested. Also the number of attacks per host as a function of the number of parasitoids per host falls significantly below that expected if the attacks of the parasitoid were distributed at random and shows a close fit to $K = 2$ (Fig. 5). Finally the slopes of $\log_e K$ as function of parasitoid density or of time do not depart significantly from 0. Thus we conclude, as did Griffiths and Holling (op.cit.), that K is a constant for the system. It is probably a measure of the ability of the host to escape parasitism at the higher parasite densities and thus counteract the instability resulting from the explicit lag in the parasitoids response. So, at the outset, this host-parasitoid system seems to possess two very important properties of competition models: it oscillates, and the attacks of the parasitoid are described by a negative binomial distribution.

The next step in the development of the model is to calculate the survival of the parasitised population as a function of the survival vector SUPARAS and set it to year $I + 1$. The unparasitised population's survival is set as a function of the survival vector SULIV multiplied by the potential fecundity, F , and set to year $I + 1$.

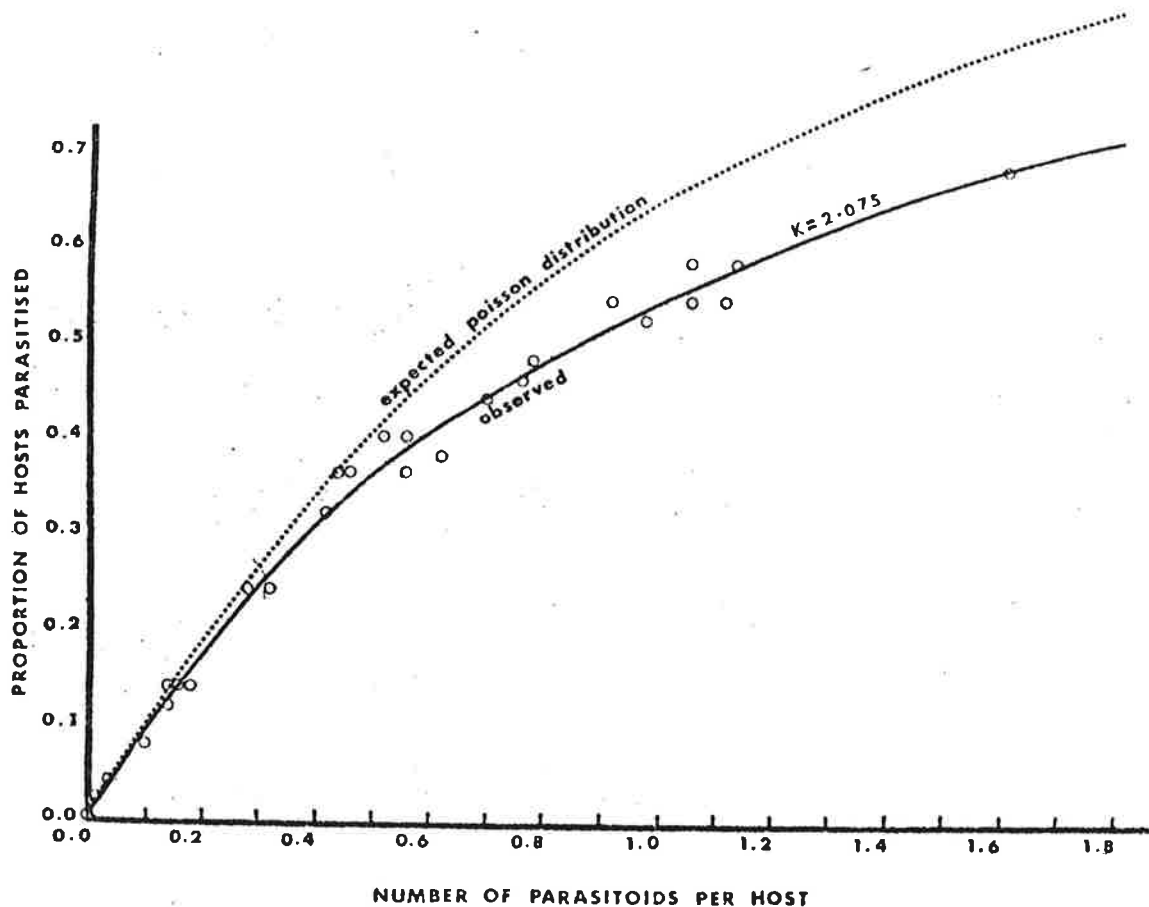


Fig. 5. Proportion of hosts attacked as a function of the number of parasitoids per host for the *Neodiprion swainei* host-larval parasitoid life system. Dotted line is proportion expected if attacks of parasite are random. Mean k of negative binomial distribution for the system is 2.075.

Note that parasitoid survival within the host is assumed to be constant at all parasitoid densities. That this may not be true was recognized by Griffiths and Holling (op.cit.); exploitation theory is well developed for the attack phase of the cycle but lacking for the interference which may result from parasitoids competing within a common host. It seems likely that the distribution of survival rates of the parasitised population would also be contagious since the probability of survival of superparasitised individuals would likely be considerably lower than that of individuals with single parasitoids. If survival rates throughout the full range of parasitoid densities is constant, a plot of the proportion of parasitised hosts in subsequent host ages as a function of the

proportion in the attacked stage should yield straight lines (Fig.6). In fact the proportion drops with increasing rate of attack, implying that the more heavily attacked hosts are more prone to mortality from agents other than the parasitoids themselves. The stress resulting from the presence of supernumary parasitoids would also decrease the probability of survival. A future development of this host-parasitoid model will be the derivation of a mathematical expression to describe these processes.

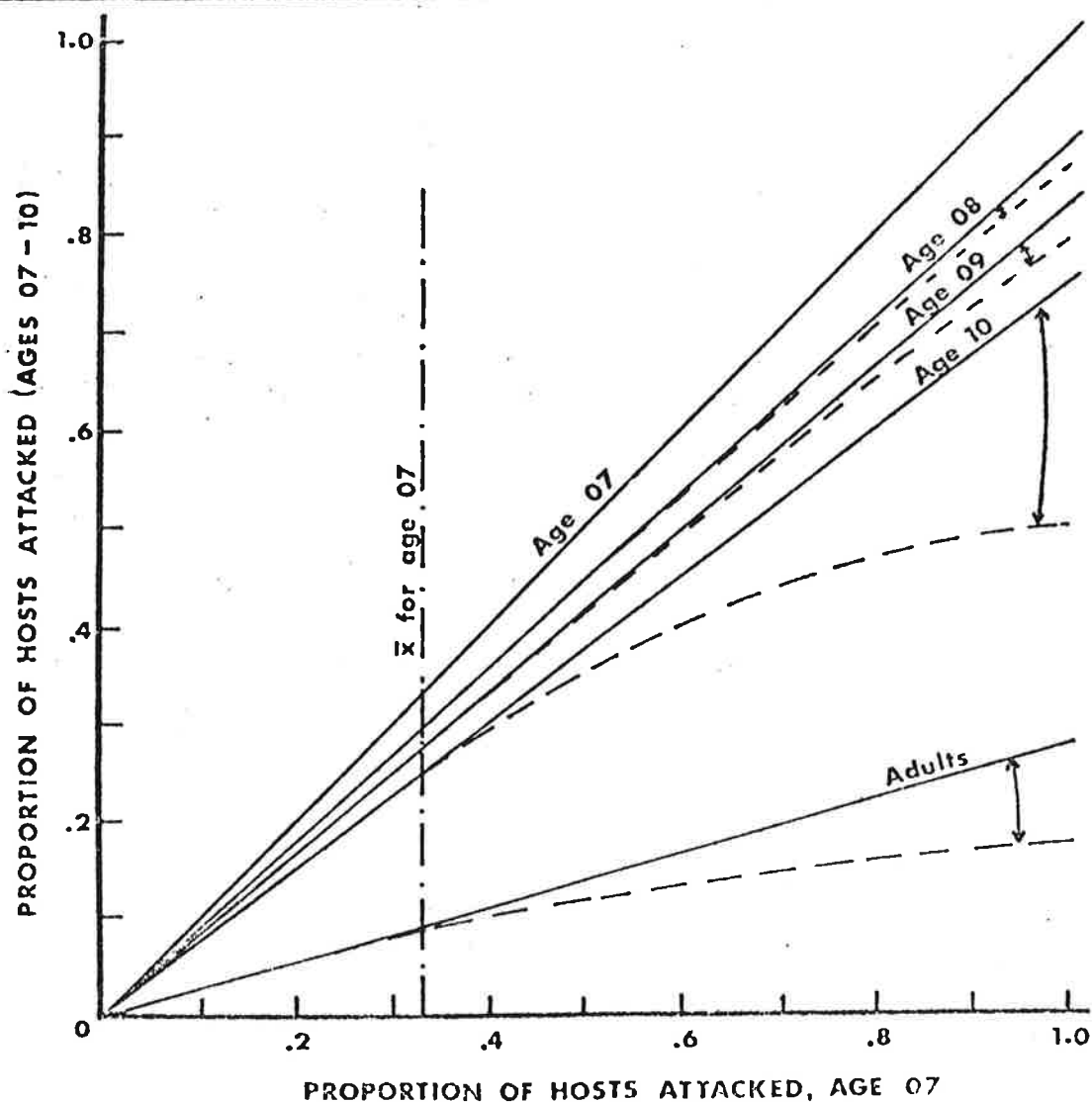


Fig. 6. Proportion of hosts attacked by larval parasitoids in host ages 07, 08, 09 and 10 as a function of hosts attacked in age 07. Survival rates of parasitoids, if constant, should yield straight lines. The dotted lines are approximations to the observed trends. Age 07 = mature larva, age 08 = pre-spinning eonymph, age 09 = cocoon (fall) and age 10 = cocoon (spring).

The last step in the recursion is to increment the population according to the logistic function (5). Since we have, by definition, established that the parasitoids are the only regulators, then the intrinsic rate of increase is just that which would hold in the absence of the parasitoids, in this case 1.464 per annum. The upper limit of the hosts population growth has been tentatively set at 600 eggs per sq. metre pending more detailed analyses which are forthcoming. This is the level at which replacement of foliage will just balance the amount defoliated without loss of quality, or about 60 percent defoliation i.e. when most of the current years' foliage is untouched.

The model's output includes a graph of host density, parasitoid progeny density, and percentage parasitism as a function of time, as well as a phase diagram for parasitoid density as a function of host density. A plot of parasitoid progeny and host density as a function of time is shown, (Fig.7)

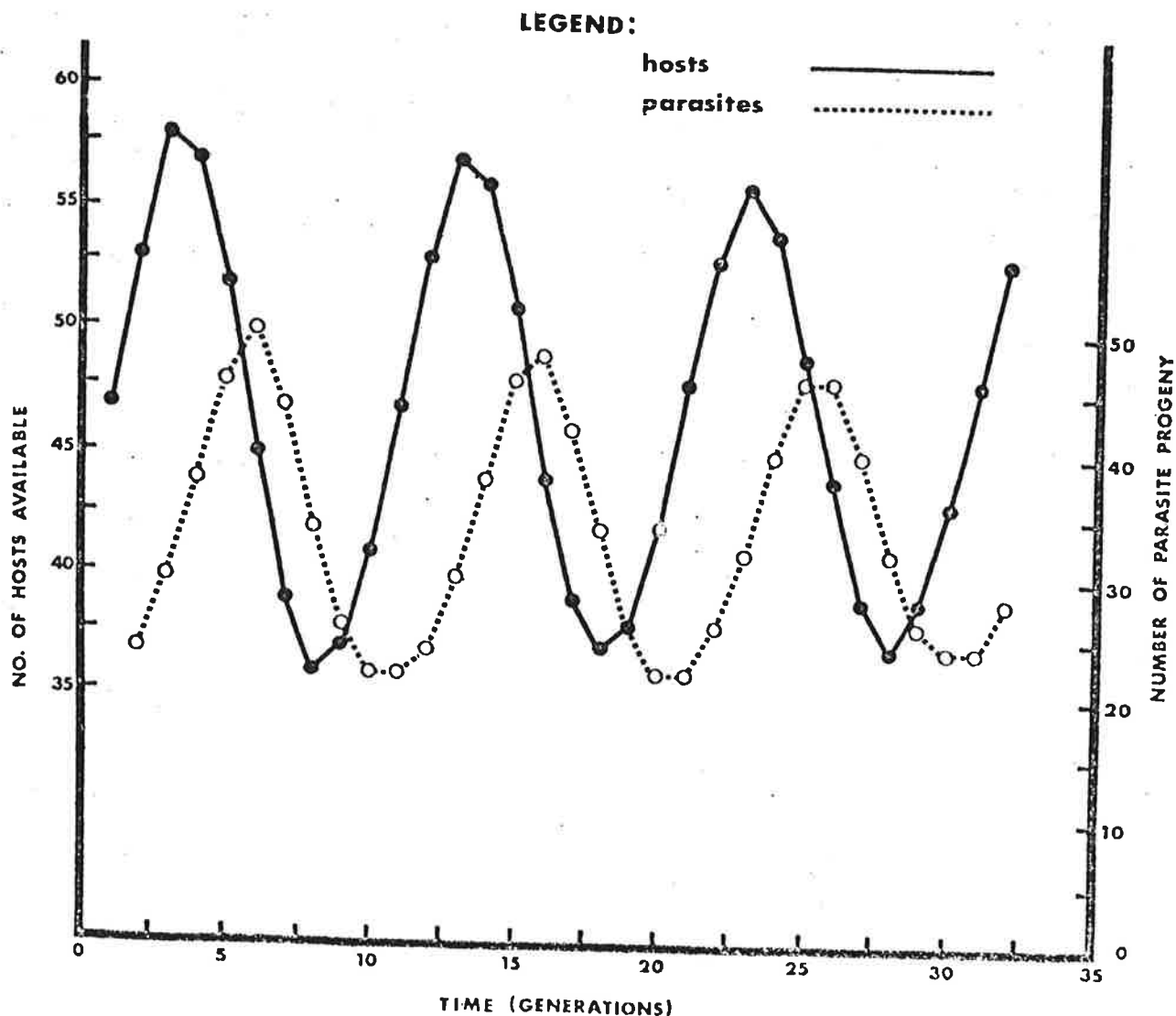


Fig.7. Output from *Neodiprion swainei* competition model showing host density (HN) and parasitoid progeny density (PN) as a function of time (generations). Parameters are listed in Tables 1 and 2.

Table 3. Regression statistics for predicted vs observed (output from competition model) populations in the Neodiprion swainei host-larval parasitoid life system. $df = 10$

Variable	Regression Equation	r	t
Host populations	$y = 38.08 + .1061 X$.27	1.93
Parasitoid populations	$y = 23.31 + .3997 X$.59	3.83 **
Parasitoids per host	$y = .5394 + .3377 X$.72	5.03 **

**p < .01

How closely does the model mimic reality? It is a surprisingly good predictor of parasitoid population trends but a rather poor predictor of host trends (Table 3), and underestimates the amplitude of both host and parasitoid oscillations. It is a naively simple model in that only the larval parasitoid group is considered. I chose to analyse the group before individual species because the strongly synchronized trends indicated that the larval parasitoids were acting as a "block" or "unit" and it would be of interest to analyse role of the group before considering the individual species. Further justification for considering the species group or guild as a valid population unit are given by Root (1968) and May (1972b). Parasitoid mortality within the host has been only partly analysed. The encapsulation response of the host to parasitoids shows a sigmoid rise to a plateau of about .5 parasitoids per host, suggesting that there is a threshold beyond which further encapsulation of supernumary parasitoids is impossible. This, as well as the contagious distribution of parasitoid survival within the host might increase instability in the host parasitoid system, and explain the higher oscillations in the observed vs the predicted trends. These results however suggest that exploitation theory may provide very good predictions of host-parasitoid population trends, and so further elaboration of the model is planned, through inclusion of the effects of competition by individual parasitoid species and of parasitoid mortality within the host. Furthermore, the value of long-term life table studies in the understanding of population interactions is clearly demonstrated.

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