

PARASITOID / HOST INTERACTION MODELS**Notes****I. Parasitoid - Host Interactions. Thompson's Model (1924)**

- A. The Lotka-Volterra equations considered populations with continuous (overlapping) generations. All life stages were assumed to be present at any one time.
- B. Mathematical models for parasitoid-host interactions consider host and parasitoid populations with discrete synchronized generations. Remember all the models we deal with make a great many assumptions about the real world and must be accepted for what they are worth based on that fact.
- C. W. R. Thompson (1924) was interested in what happened to parasitoid/host populations in areas where parasites were released into an area with a large host density (Such as in Classical BC Projects). He assumed three things:
1. The parasites would have no difficulty in finding their hosts; and
 2. The parasite's rate of increase would be limited only by the female parasite's egg supply.
 3. An additional assumption was that the parasitoid and host populations were synchronized in their generations and the generations did not overlap.
 4. In the model initially he assumed that the parasitoid would only lay one egg in each host that was found. Thus:

(No. eggs laid) = (Mean Female Egg Compliment)(No. Females Searching)

$$P_e = (C) \times (P)$$

5. However, this model did not work too well because many parasites are unable to distinguish between parasitized and unparasitized hosts. Thus Thompson's model predicted a higher rate of parasitism than would actually occur. In reality, a host can end up with more than one parasitoid egg and is then "superparasitized".
- D. Thompson next assumed that the encounters between parasites and hosts were distributed at random. He used a random distribution formula to calculate the number of hosts attacked. The formula took the form:

$$N_{ha} = N [1 - e^{-(N_e/N)}]$$

where N_{ha} = the number of hosts attacked; N = the number of hosts present; and N_e = the number of hosts encountered;

Unfortunately the model caused the host and parasitoid population to go to extinction (everything died) (Fig. 12.1). The populations did not oscillate or cycle.

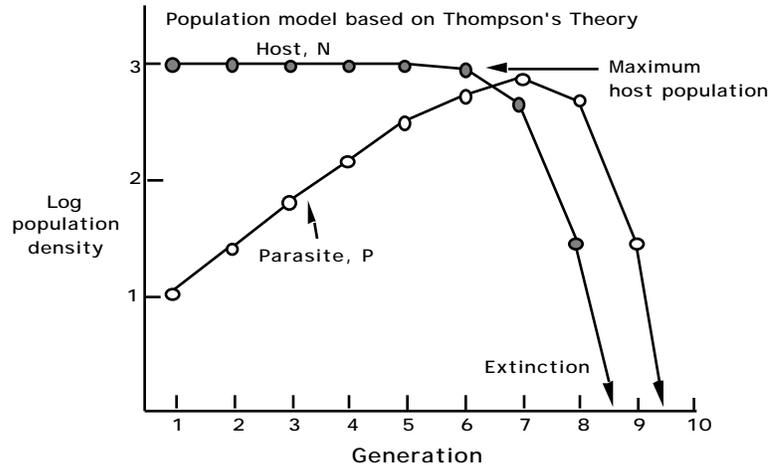


Fig. 12.1. Population model for a stabilized host population attacked by a parasite using Thompson's theory. Host reproductive rate (F) = 2, population stabilized by a density dependent factor at 1000. Parasite lays an average of 2.5 eggs. Figure modified from Varley *et al.* (1974).

Notes

E. Thompson's model was not a good description of parasitoid/host interactions when the situation occurred in which the hosts were comparatively rare and the parasite's searching ability became important. When "unparasitized" hosts became rare many of the previously parasitized hosts were attacked more than once. Some greater than 8 times at a host density of 100 per unit area. See table below and figure 12.2 at top of the following page.

Number of attacks per host at a host density of 100 hosts per unit area required by a parasitoid using Thompson's strategy of random encounter to obtain 99% host mortality¹.

No. Attacks per Host	Frequency	No. Hosts Attacked per 100 Hosts	Surviving Progeny	Eggs Wasted
0	0.01	1	0	0
1	0.06	6	6	0
2	0.13	13	0	26
3	0.18	18	0	54
4	0.19	19	0	76
5	0.16	16	0	80
6	0.12	12	0	72
7	0.07	7	0	49
8	0.04	4	0	32
9	0.02	2	0	18
10	0.01	1	0	10

¹ Note that any host attacked more than once is superparasitized and will die according to the assumptions of this model. Thus in this situation 98.6% of the eggs will not develop due to superparasitism. Also note that in a situation like this 423 eggs have to be laid in order to parasitize 99% of the hosts. Only 6 progeny survive in this situation (see figure next page).

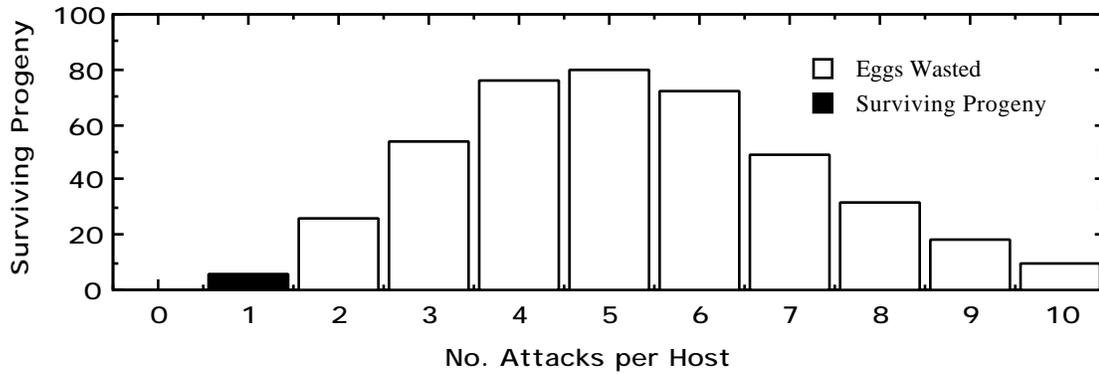


Fig. 12.2. Results of Thompson model showing low numbers of surviving progeny due to superparasitization.

Notes

II. Parasitoid - Host Interactions. Nicholson and Bailey's Models.

- A. Unlike Thompson, who looked at situations where a parasitoid species was released into an area of high host density, these researchers assumed that the parasitoid and its host were in a "steady state" (parasites and host coexist in a state of equilibrium) in their models.
- B. Several assumptions were made:
 1. Parasites would search for their hosts at random;
 2. The ability of the parasitoid population to grow in size was not restricted to their egg supply, but to their ability to find hosts. Further assumptions were:
 - a. the rate at which the parasites find their hosts was proportional to the host density (the parasites egg supply was never a limiting factor); and
 - b. the average area which one parasitoid searches in its lifetime was constant and characteristic for that species. Referred to as the "area of discovery" or "a" (for short)(Fig. 12.3).
- C. The basis of all the Nicholson-Bailey Models was the "competition curve" (Fig. 12.3). Literally this mathematically expressed the idea that the percentage of parasitism increased towards the 100% level as the parasitoid density increased.
- D. The area of discovery (a) was equal to the width of track along which the parasitoid searched multiplied by the length of track accumulated through the parasite's lifetime. Thus:

$$\frac{\text{area traversed for}}{\text{population of parasites}} = a P;$$

where a = area of discovery and P = parasitoid density. The assumption was made that groups of individuals not searching systematically will be searching at random.

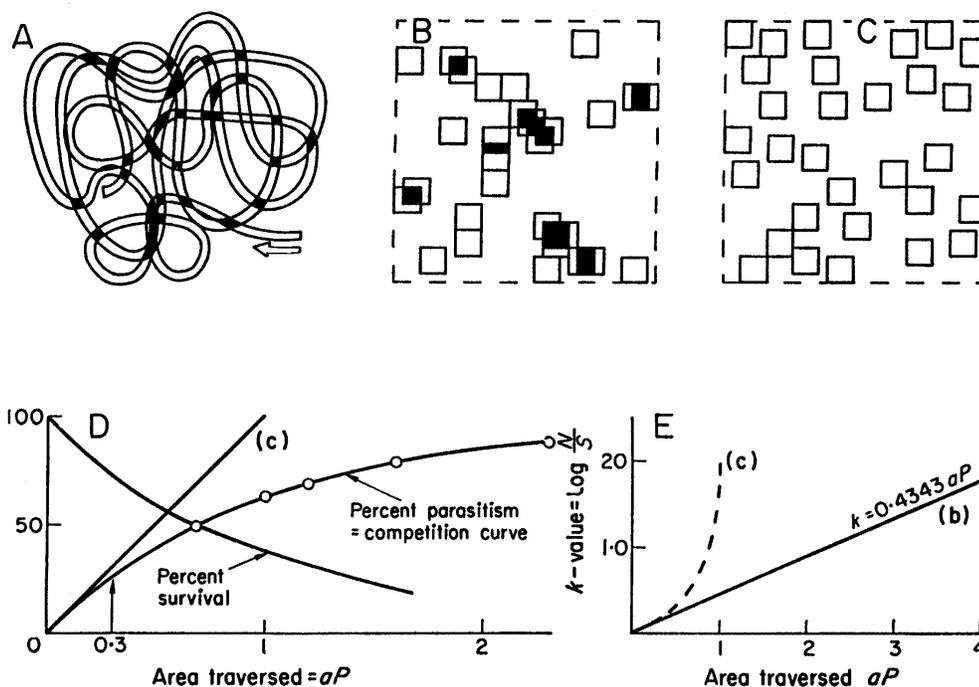


Fig. 12.3. A. Hypothetical track of randomly searching parasite.
 B. Schematic representation of 30 parasites searching in a given area. Each square represents the area of discovery (0.01 of total area) of a single parasite.
 C. As B, but parasites search systematically by avoiding areas previously traversed.
 D. Nicholson's "competition curve." The straight line (c) would be obtained if the parasites searched systematically.
 E. As D, but parasitism expressed in k -values to illustrate derivation of equation.
 Figure from Varley *et al.* (1974).

Notes

E. Estimates of the "area of discovery" can be made from field data if one knows:

1. The density of the parasites searching (P);
2. The density of the hosts (N); and
3. The density of hosts not parasitized (S) (This equals Total Hosts minus Parasitized Hosts).

The equation is:

$$a = \frac{\ln N/S}{P} ; \quad aP = \ln (N/S)$$

F. Other helpful formulas to know are:

$$\text{Killing Value} = \text{Log } N/S = (aP) / 2.3 = 0.4343 aP$$

(log % Kill)

G. If one knows the current pest density (N_t), parasitoid density (P_t), host reproductive rate (F_h) and area of discovery (a); then one can produce an equation to predict the densities of the next generation ($t + 1$) of hosts (N_{t+1}) and parasites (P_{t+1}):

Notes

Next Host Generation:

$$\text{Log } N_{t+1} = \text{Log } N_t - [(aP_t) / 2.3] + \text{Log } F_h$$

Next Parasitoid Generation:

$$P_{t+1} =$$

$$N_{ha} = N_t - \text{antilog}_{10} \{ \text{Log } N_t - [(aP_t) / 2.3] \}$$

For example, if host density = 25; host fecundity = 2.5; parasitoid density = 11; and parasitoid area of discovery = 0.068, then the following calculations would be appropriate:

Generation No. (N_t)	Host Density	Log Host Density	Parasitoid Density	Log N_{t+1}	N_{ha}
1	25.00	1.40	11.00	1.37	1.12
2	23.66	1.37	13.17	1.29	1.14
3	19.33	1.29	13.99	1.17	1.07
4	14.92	1.17	11.90	1.12	0.91
5	13.31	1.12	8.26	1.18	0.75

Notes

H. Problems with the Nicholson-Bailey Model:

1. The model is unstable. Both the parasitoid and host go to extinction. The parasitoid wipes out the host and then dies due to a lack of host material (sounds something like Thompson's model, huh??) (Figs. 12.4, 12.5).
2. The model does not work in a direct density dependent manner, but in a delayed density dependent manner. This has been referred to as the effect of a "Nicholsonian parasitoid" - delayed density dependent mortality (Fig. 12.6).

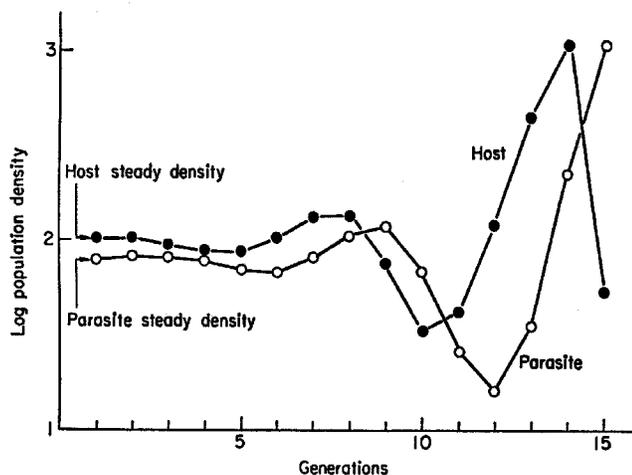


Fig. 12.4. A population model based on Nicholson's theory. From Varley *et al.* (1974).

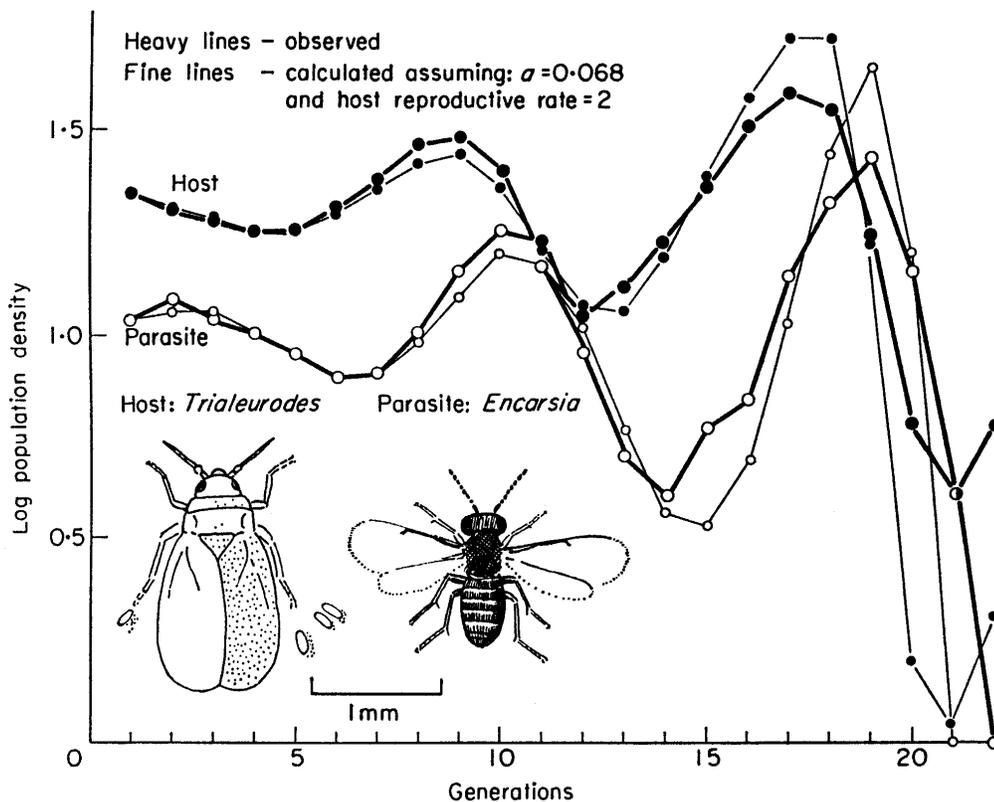


Fig. 12. 5. Observed and calculated results of an interaction between *Encarsia formosa* and the greenhouse whitefly *Trialeurodes vaporariorum*. Model calculated on basis of a constant area of discovery of 0.068 and a host reproductive rate of 2. From Varley et al. (1974); see for more details.

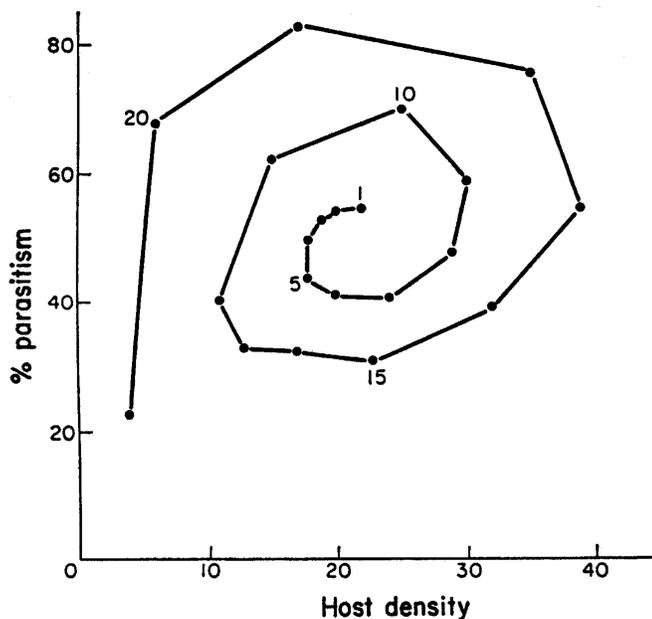


Fig. 12. 6. An example of delayed density dependent mortality. Numbers adjacent to plotted line indicate generation number. From Varley et al. (1974).

Notes

- I. Stabilization for the Nicholson-Bailey Model. The model may be stabilized by adding a density dependent factor such as intraspecific competition between individuals of the parasitoid species. See "handling time" and "interference" in next lecture notes. Stabilization was somewhat achieved by adding interspecific competition in the form of additional primary parasites and hyperparasites.

QUESTIONS

1. Thompson's model did not simulate parasitoid / host population interactions well. Why not?
2. What is "area of discovery"? Why is it important to the success of a natural enemy? What information does one need to calculate area of discovery for a parasitoid from field data?
3. What is a "Nicholsonian parasitoid"?
4. What purpose do models serve? Why do we study them?

REFERENCES

- Berman, S. M. 1974.** Calculus for the nonphysical sciences with matrices, probability and statistics. Holt, Rinehart and Winston, Inc., N. Y. 656 pp.
- Huffaker, C. B. & P. S. Messenger. 1964.** Population ecology - historical development. p. 45-73. *In* Biological Control of Insect Pests and Weeds (P. DeBach, editor). Chapman and Hall Ltd., London. 844 pp.
- Pianka, E. R. 1974. Evolutionary ecology.** Harper & Row, Publ., N. Y. 356 pp.
- Pielou, E. C. 1977.** Mathematical ecology. John Wiley & Sons, N. Y. 385 pp.
- Price, P. W. 1975.** Insect Ecology. John Wiley & Sons, N. Y. 514 pp.
- Varley, G. C., G. R. Gradwell & M. P. Hassell. 1974.** Insect population ecology - an analytical approach. Univ. Calif. Press, Berkeley and Los Angeles. 212 pp.
- van den Bosch, R., P. S. Messenger & A. P. Gutierrez. 1982.** An introduction to biological control. Plenum Press, N. Y. 247 pp.
- Van Driesche, R. G. and T. S. Bellows, Jr. 1996.** Biological control. Chapman and Hall, New York. 539 pp.
- Vandermeer, J. 1981.** Elementary mathematical ecology. John Wiley & Sons, N. Y. 294 pp.
- Wilson, E. O. & W. H. Bossert. 1971.** A primer of population biology. Sinauer Associates, Inc. Publ., Stamford, Conn. 192 pp.

READING ASSIGNMENT:

- Chapter 18: pp. 367-398, **Van Driesche, R. G. and T. S. Bellows, Jr. 1996.** Biological control. Chapman and Hall, New York. 539 pp.