

**FACTORS LIMITING PARASITISM***Notes***I. Parasitoid - Host Interactions. Interference in Searching.**

- A. Several factors may stabilize population interactions between natural enemies and their hosts (or prey). One stabilizing factor is interference in searching when parasites contact each other at high densities while searching for hosts or prey. This is a form of intraspecific competition.
- B. When two parasites (same species) meet in an area while searching for hosts:
1. Usually one or both will leave the area;
  2. This decreases searching efficiency; and
  3. This occurrence increases as parasitoid density increases.
- C. Hassell and Varley (1969) proposed a model to estimate the amount of interference in a population at different Parasitoid densities. It was:

$$\log "a" = \log Q - (m) \log P \quad (1)$$

where "a" = area of discovery; Q = "the Quest constant"; m = the "mutual interference constant"; and P = parasitoid density.

- D. The Quest constant equals the area of discovery when the parasitoid density is 1 per unit area. Note: when P = 1; log P is zero (Fig. 13.1).
- E. In Nicholson's model his assumption of "constant searching efficiency" would be a case where the interference constant "m" is equal to zero. Adding "interference" into a Nicholsonian model can make it stable. The more "interference" the more stable it becomes.

**II. Parasitoid - Host Interactions. Functional and Numerical Responses.**

- A. Responses that natural enemies display with respect to their host populations may be regarded as immediate or delayed. Immediate responses have been referred to as "functional" responses (Fig. 13.3). Delayed responses are referred to as "numerical" responses (Fig. 13.3).
- B. Functional Response: changes in the number of attacks per parasitoid (or predator) as host (prey) density changes. This is an inverse density dependent factor (as the host increases the response decreases).
- C. Studies indicate that "handling time" has an important effect on the functional response. Handling time is the time interval that elapses from the first encounter of a host by a natural enemy until the time when the search is resumed. This time can vary considerably between species (20 seconds to several hours). Concept explored through use of the Holling Disk Equation which is:

$$N_a = [a N T P] / [1 + (a T_h N)] \quad (2)$$

where  $N_a$  = number of hosts attacked (discs);  $a$  = attack rate (expressed

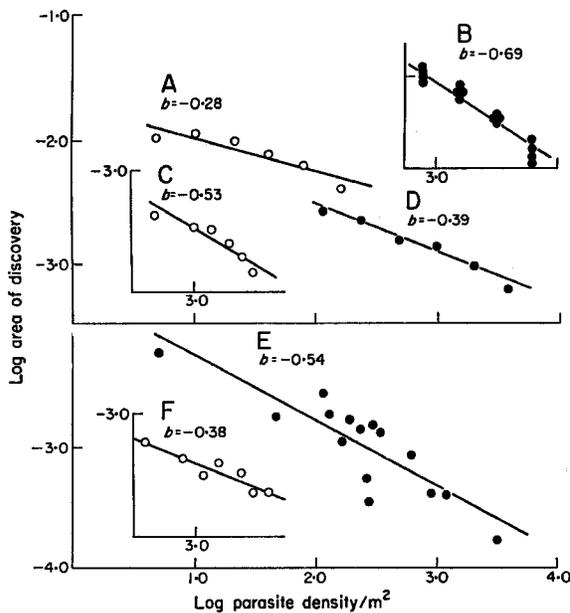


Fig. 13.1. Relationships between log area of discovery and log density of searching parasitoids: A) *Dahlbominus fuscipennis*; B) *Pseudeucoila bochei*; C) *Chelonus texanus*; D) *Encarsia formosa*; E) *Nemeritis canescens*; and F) *Cryptus inornatus*. Figure from Varley *et al.* (1974); see for more details.

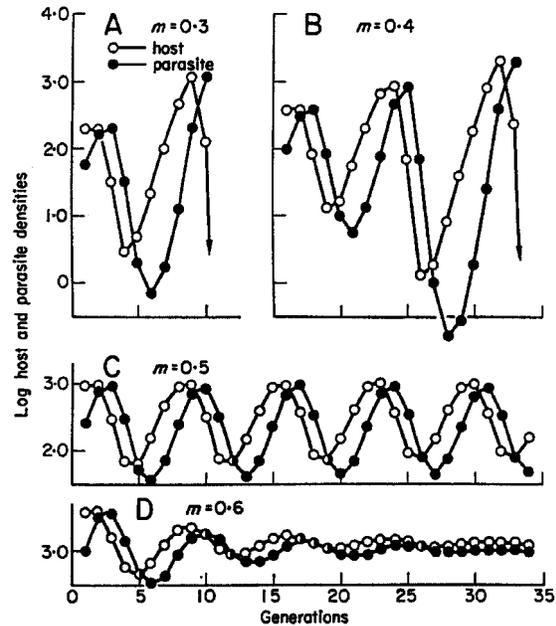


Fig. 13.2. Population models showing the increasing stability as the mutual interference constant  $m$  is increased from 0.3 in A to 0.6 in D. Figure from Varley *et al.* (1974); see for more details.

where  $N_a$  = number of hosts attacked (discs);  $a$  = attack rate (expressed as hosts attacked/time);  $T$  = total searching time;  $P$  = number of predators; and  $T_h$  = handling time (total amount of time spent removing discs from arena and placing them in receptable). Please note that the attack rate ( $a$ ) in Holling's equation differs from the area of discovery ( $a$ ) in the Nicholson/Bailey Model.

- D. The proportion of the total time spent in handling hosts increases as more hosts are found (as host density increases)(Fig. 13.3). This reduction in time spent searching at high host densities reduces searching efficiency. Handling time alone may limit the maximum attack rate per parasitoid at high host densities (see figure on following page).
- E. The models examined reflect different assumptions about the relationship between the number of hosts killed vs. host density.

1. Thompson's Model. No change in host kill with increase in host density.
2. Nicholson-Bailey Model. Ability to kill hosts was a constant as host density increased.
3. Holling Model. Functional response curve - host kill reduced as host density increases.
4. Sigmoid Curve. Predator learns to recognize prey and handling time is reduced as prey density increases.

Notes

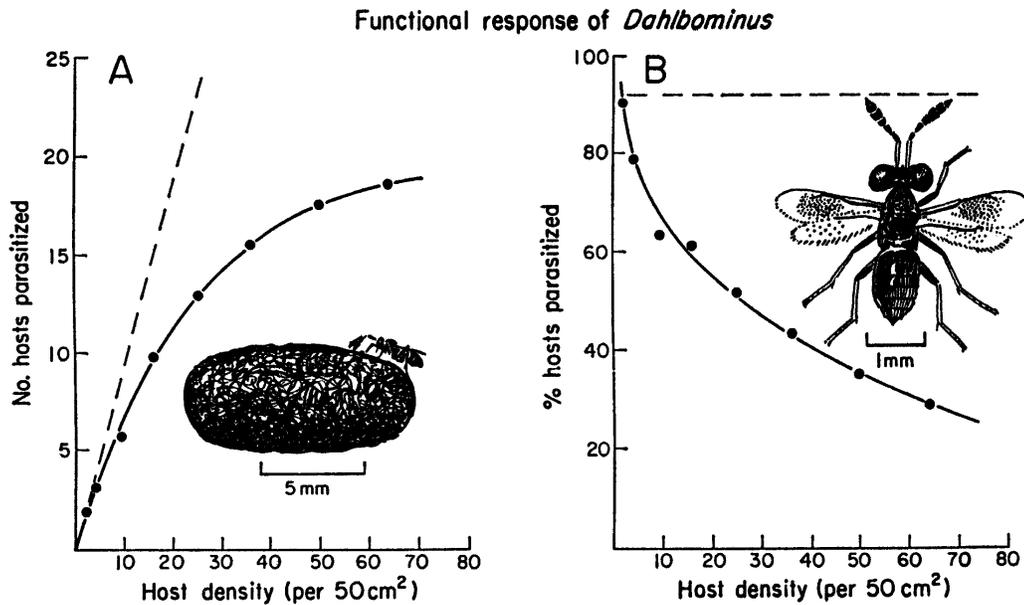


Fig. 13.3. The functional response of a single female of the chalcid parasite *Dahlbominus fuscipennis* searching for cocoons of the saw-fly *Neodiprion sertifer* within cages of 50 cm floor area. A = Functional response expressed as the number of hosts parasitized at different host densities; and B = Functional response expressed as the percentage of hosts parasitized at different host densities. The broken line shows the response expected of a Nicholsonian parasitoid. Figures from Varley et al. (1974); see for more details.

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- F. Numerical Response: increase in parasites with increase in host population density (Fig. 13.3). This is basically the parasite's birth rate which is a function of the prey or host death rate. This factor is intimately linked to the functional response. Together these 2 responses influence the prey or host population dynamics with intermediate and delayed responses.

## VI. Conclusions.

The models we have examined emphasize that in real life situations the higher the searching efficiency the lower the equilibrium density of the parasitoid and its host. Factors which limit searching efficiency can actually stabilize the population interactions.

## VII. Competition Between Natural Enemies

- A. Competition is the active demand by 2 or more organisms for a common vital resource. This only occurs when the resource is in short supply and thus becomes a limiting factor in population growth.
- B. As stated previously, there are two types:
1. Intraspecific (between individuals of one species)
  2. Interspecific (between individuals of 2 species)
- C. All species occupy a "niche" in the environment. A niche is the place or position, in both a physical and a functional sense, of a species population in an ecosystem as determined by the full complex of environmental factors impinging on and limiting the population. Odum

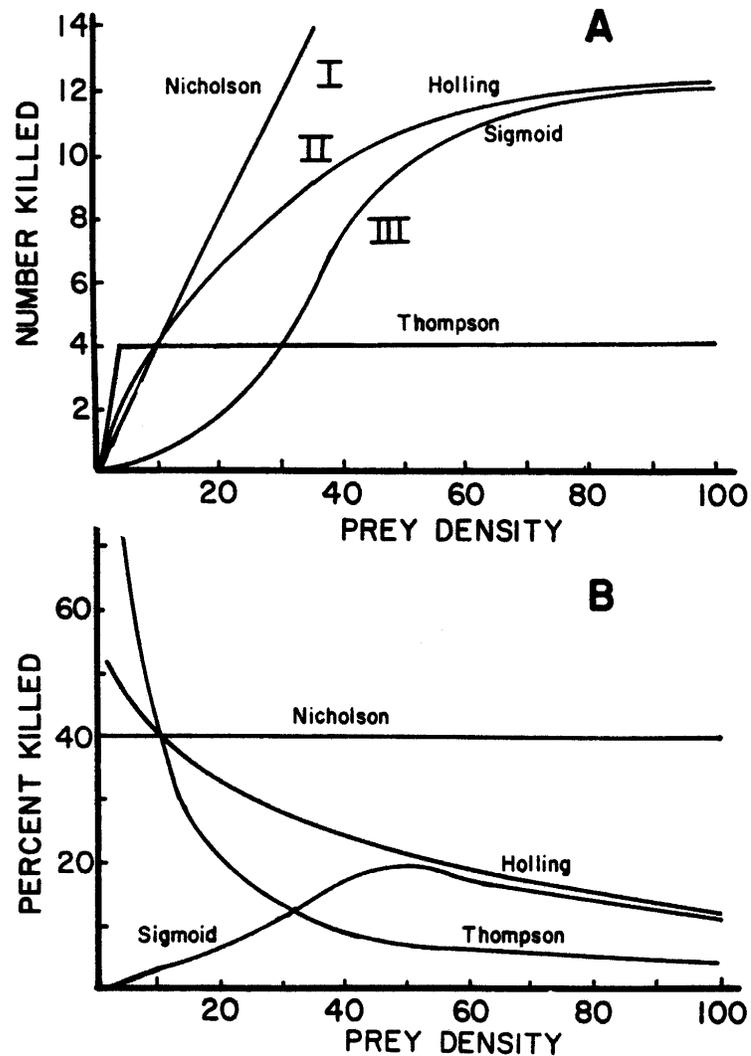


Fig. 13.4. Various proposed functional response models depicting (A) the number of prey killed as a function of prey density, and (B) the percentage killed as a function of prey density. See Varley et al. (1974) for more details.

### Notes

- stated that "the habitat is the organism's address, whereas the niche is its "profession".
- D. In the environment one may find "generalists" and "specialists". Generalists are better able to accept environmental changes than specialists.
- E. "Hypervolume" model - there can be more than 3 environmental gradients with respect to environmental requirements for an organism.
- F. If two species are similar enough to each other in their requirements (or niches), then one will go to extinction due to competition. Species in these situations have been referred to as "ecological homologs". This principle is known as:
1. Gause's Principle;
  2. Grinnell's Axiom;
  3. Competitive Exclusion (or Displacement) Principle; and
  4. Volterra - Gause Principle

## Notes

- G. Thus, unless the niches of 2 species (in the same location) differ, then the species cannot coexist. One will go to extinction due to competition. Two species can be genetically different, but end up in a particular environment where they are forced to live together.
- H. Competitive exclusion occurs if one species produces enough individuals to prevent the population of the 2nd species from increasing. Competitive exclusion will not happen if the two niches are different enough that each species enjoys a portion of the environment where it can not be suppressed by excessive numbers of its competitors.

## I. EXAMPLES:

1. *Aphytis chrysomphali*, *A. linganensis*, and *A. melinus* attacking California red scale (*Aonidiella aurantii*) in Southern California. These species competed with respect to climatic conditions (Figs. 13.5-.6).
  - 1959 - *A. linganensis* displaced *A. chrysomphali* in interior regions
  - 1965 - *A. melinus* displaced *A. linganensis* in high desert regions
2. *Biosteres (Opus) longicaudatus*, *B. vandenboschi*, and *B. oophilus* attacking the Oriental fruit fly (*Bactrocera dorsalis*) in Hawaii. These species competed with respect to suitable hosts (Fig. 13.7).
  - 1950 - *B. vandenboschi* displaced *B. longicaudatus* due to former's ability to parasitize younger stages of larvae
  - 1951 - *B. oophilus* displaced *B. vandenboschi* due to former's ability to parasitize eggs

## QUESTIONS

1. How did Hassell & Varley envision the relationship between interference and area of discovery? Provide a mathematical description and a graphical one.
2. What is "handling time"? What is its importance in the functional response of natural enemies?
3. What is the relationship between functional response and numerical response?
4. What is the "hyper volume" model?
5. Why is the principle of "ecological homologs" important in biological control?

## REFERENCES

- DeBach, P., D. Rosen & C. E. Kennett. 1971.** Biological control of coccids by introduced natural enemies. pp. 165–194. In "Biological Control" (C. B. Huffaker, ed.), Plenum Publ. Co., New York.
- 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, and 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.

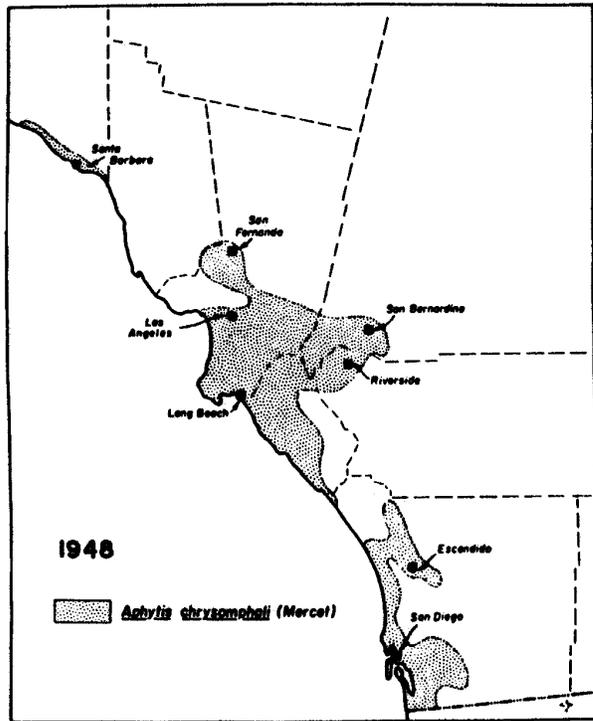


Fig. 13.5. Abundance of the California red scale parasitoid *Aphytis chrysomphali* in 1948 in Southern California prior to the introduction of *Aphytis lingnanensis*. From DeBach *et al.* (1971).

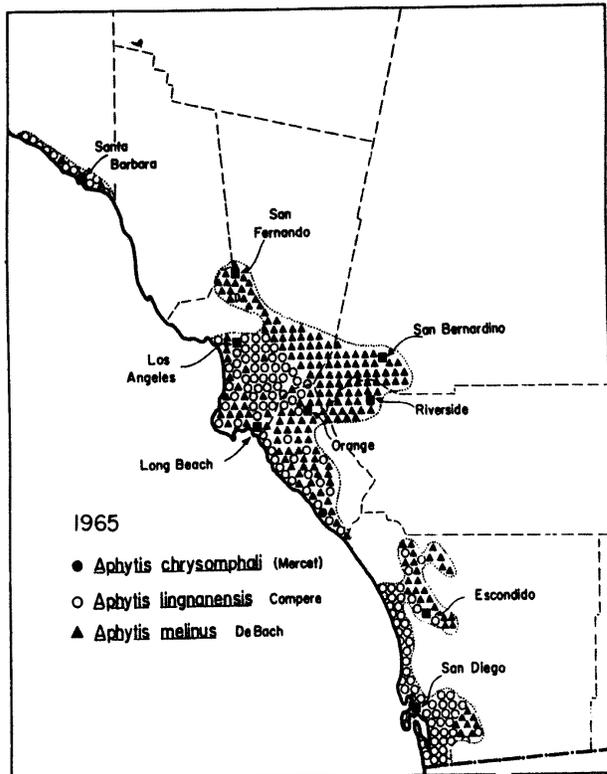


Fig. 13.6. Abundance of the California red scale parasitoids *Aphytis chrysomphali* and *Aphytis lingnanensis* in 1965 after introduction and spread of *Aphytis melinus*. Note that *A. melinus* displaced both parasitoids from the interior areas of Southern California. *A. chrysomphali* is difficult to find along the coast at this time. From DeBach *et al.* (1971).

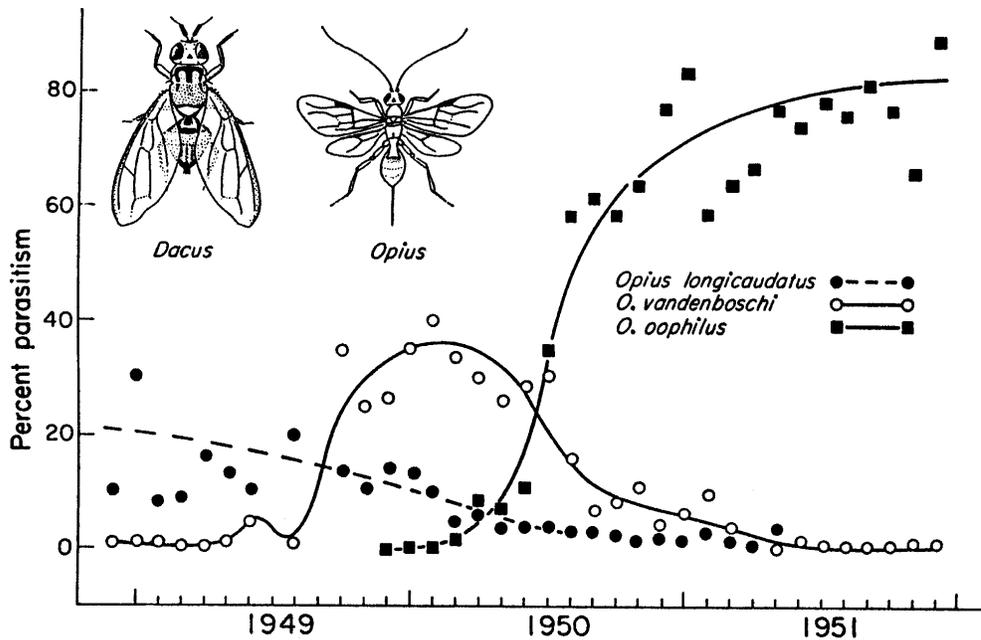


Fig. 13.7. Parasites of the Tephritid fruit fly *Bactrocera dorsalis* (= *Dacus dorsalis*) (Oriental Fruit Fly) successively established in Hawaii for biological control of this pest provide as illustration of competitive elimination. Figure from Varley *et al.* (1974); see for more details.

**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.