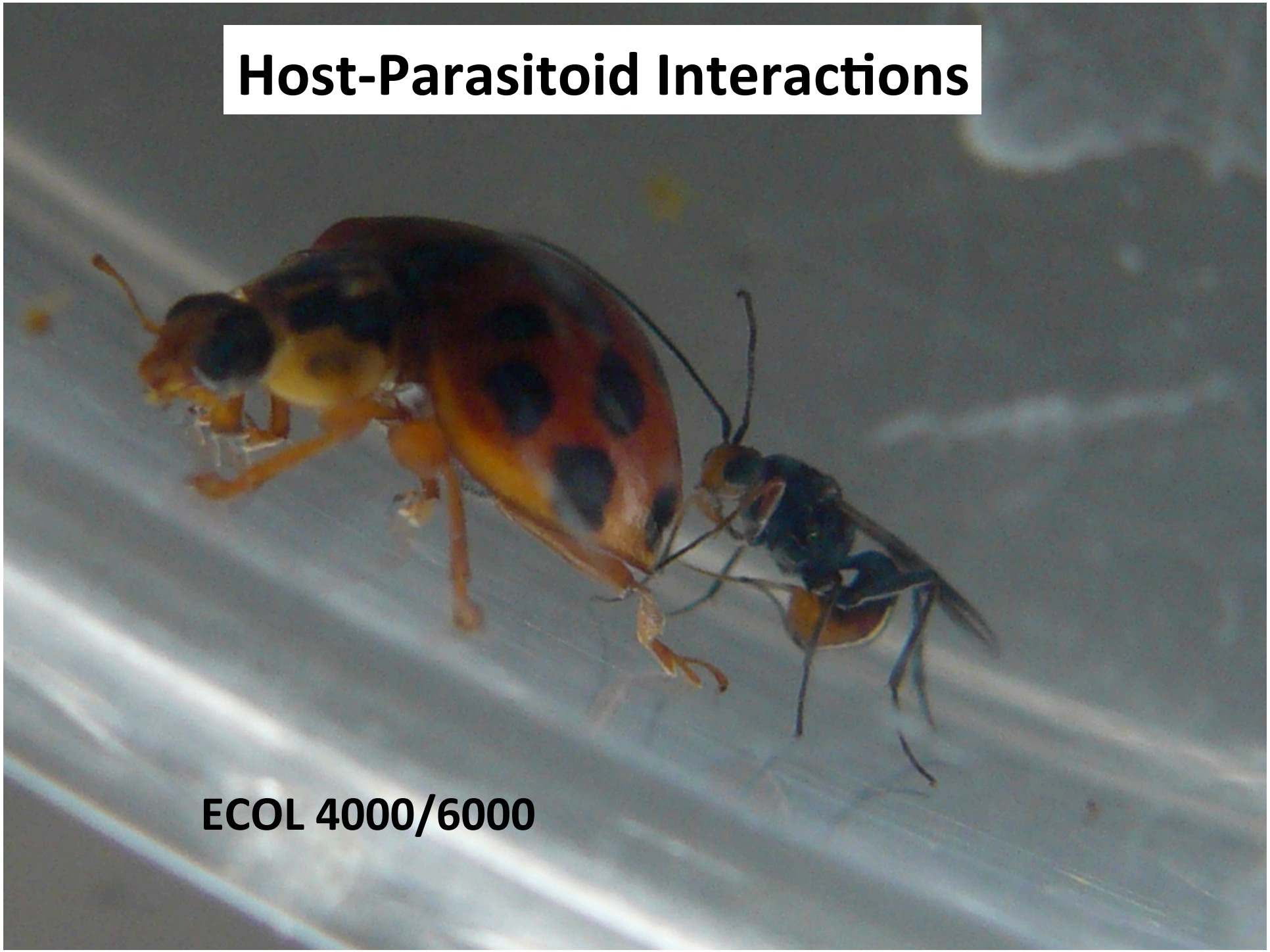
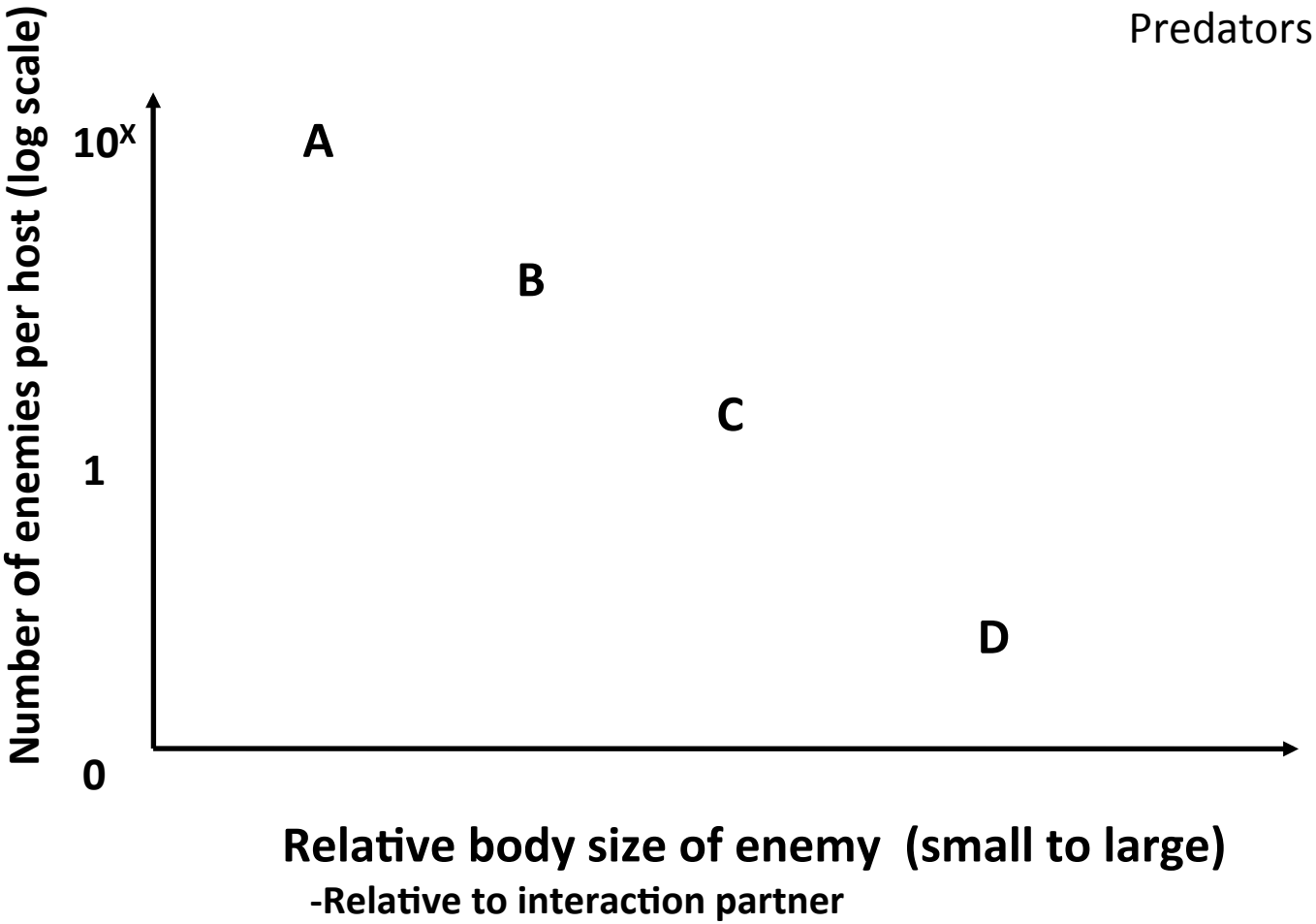

Host-Parasitoid Interactions
ECOL 4000/6000

The hierarchy of natural enemies

Assign each letter (A-D) the name of one of these four natural enemies:

Macroparasites
Parasitoids
Microparasites
Predators



The hierarchy of natural enemies

Predator (vertebrates, invertebrates): kills and then feeds on prey, similar size to, or larger than, prey

Macroparasite (ticks, nematodes): feeds in or on host, has free-living stage, occasionally lethal, small compared to host

Microparasite (viruses, bacteria, fungi): multiplies inside or on a host, occasionally lethal, very small compared to host

The hierarchy of natural enemies

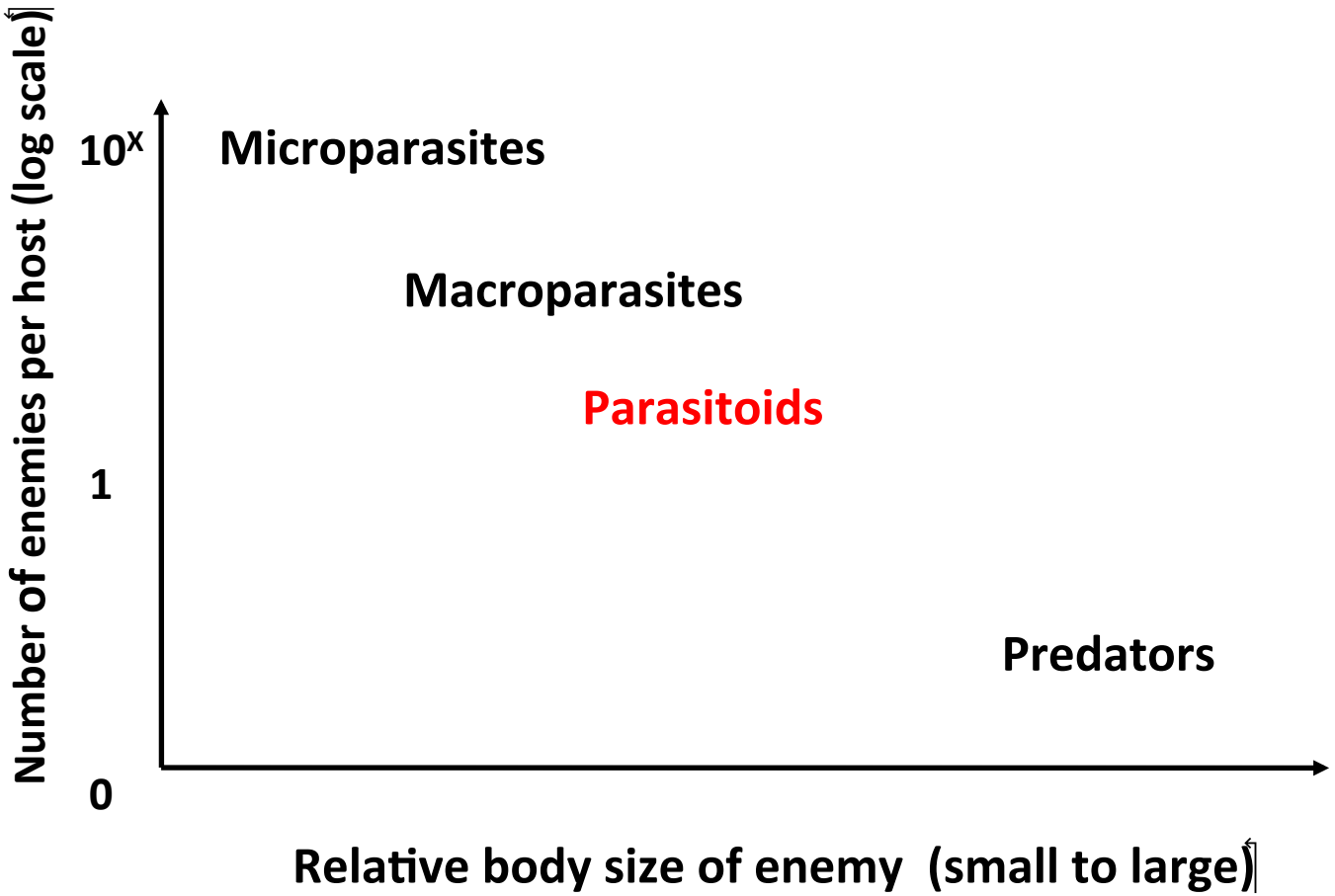
Predator (vertebrates, invertebrates): kills and then feeds on prey, similar size to, or larger than, prey

Parasitoid (insects): lays eggs in or on host, larvae feed on host, eventually killing it, similar size compared to host

Macroparasite (ticks, nematodes): feeds in or on host, has free-living stage, occasionally lethal, small compared to host

Microparasite (viruses, bacteria, fungi): multiplies inside or on a host, occasionally lethal, very small compared to host

The hierarchy of natural enemies



Parasitoid fun facts

10% of described insects are parasitoids

Mostly Hymenoptera (wasps) or Diptera (flies)

Can be host specialists or generalists

Example of life-cycle: *Dinocampus coccinellae*

Braconid wasp, attacks adult ladybird beetles
http://www.youtube.com/watch?v=qEAGistADIA

1. Searches for ladybird beetle host by probing with antennae

Example of life-cycle: *Dinocampus coccinellae*

2. Stalks host with ovipositor curved under body

Ladybird defenses: run/fly away; crouch

Example of life-cycle: *Dinocampus coccinellae*

3. Oviposits single egg into soft underbody of ladybird

Example of life-cycle: *Dinocampus coccinellae*

4. Egg hatches and larva feeds on non-essential parts of living ladybird (fatty tissue, ovarioles). When ready to emerge, larva bites through nervous system, paralyzing host

Example of life-cycle: *Dinocampus coccinellae*

5. Larva spins sticky cocoon under still-living ladybird, benefiting from host protection until adult wasp emerges

Anti-parasitoid defenses

Hosts show a range of defenses

- **Behavioral: hiding, evasion, predation!**
- **Physical: armor**
- **Chemical: defensive secretions, toxin sequestration**
- **Immune response: *encapsulation* (eggs surrounded by phagocytes and walled off from susceptible tissue)**

Cost of defense

Host: Indian Meal Moth (*Plodia interpunctella*), a stored product pest

Parasitoid: *Venturia canescens*, a Hymenopteran wasp

Individuals that successfully encapsulated are significantly smaller than unparasitized moths

Jerome Niogret, Pej Rohani

(Odum School)

Parasitoids as a biocontrol

- Parasitoids have been used to control insect pests
- Sometimes, pest is controlled by introduction of a single parasitoid species
- However, others remain pests after introduction of ten or more parasitoid species.

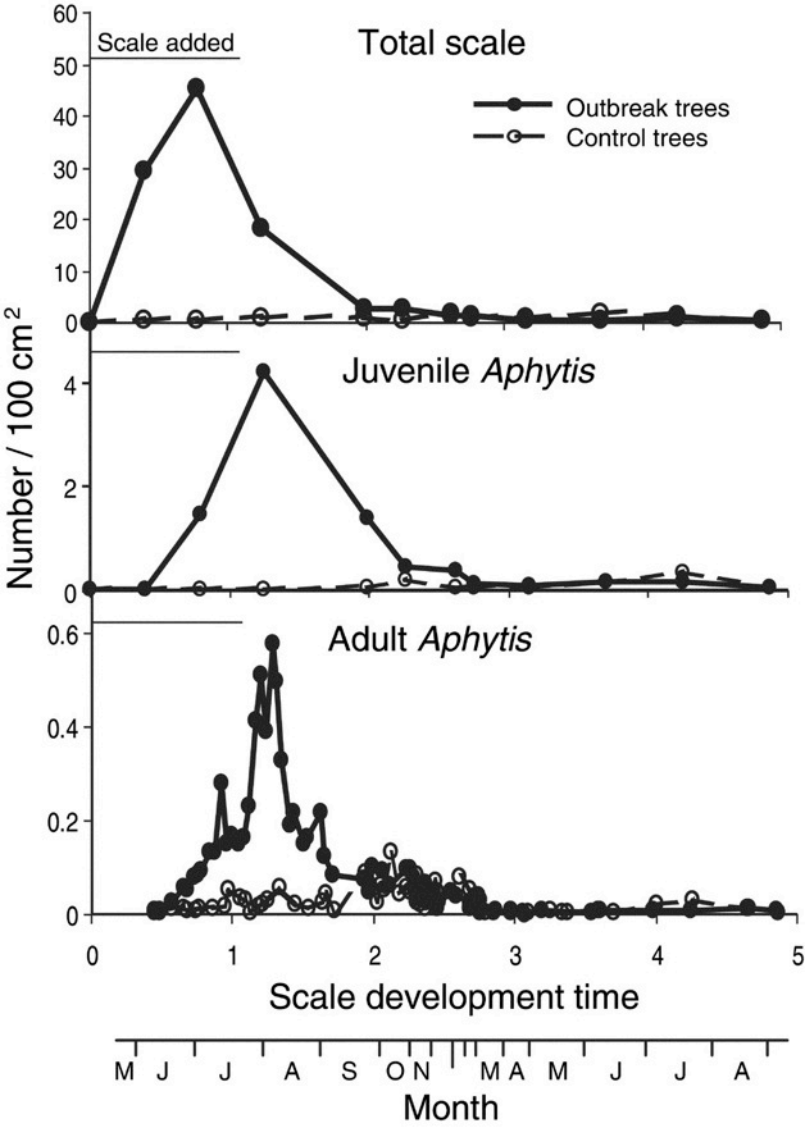
Case study: California red scale

- Pests of citrus crops worldwide
- Uncontrolled infestations can kill trees
- Almost destroyed CA citrus industry; multi-pesticide resistant
- Over 50 natural enemies introduced. Some failed to establish, others persisted locally
- In 1959, *Aphytis melinus* introduced; immediate and spectacular success

Case study: California red scale

- **Bill Murdoch and colleagues caged trees, added scales followed by adult wasps**

Case study: California red scale



- **Scale density peaked**
- ***Aphytis* density peaked**
- **Scale and wasp population crashed within 3 months, and persisted at low density**
- **Can we explain this with models?**

Nicholson-Bailey Model (1935)

- Host and parasitoid have a single generation per year, then die
- Host-parasitoid encounters occur at random
- Discrete model for host (H_t) and parasitoid (P_t) density in year t

---

- Recall $N(t+1)=\lambda N(t)$, $N(t)=\lambda^t N(0)$
- Also $N(t)=N(0)\, e^{rt}$ (solution of $dN/dt=rN$)
- So $\lambda=e^r$

Nicholson-Bailey Model - derivation

In year t+1:

- **Unparasitized hosts each produce λ new hosts**
- **Parasitized hosts each produce *c* parasitoids**
- **The probability of a host <u>not</u> being parasitized is $\phi = \phi(P_t)$**
- **The probability of a host <u>being</u> parasitized is ???**

Nicholson-Bailey Model - derivation

In year t+1:

- **Unparasitized hosts each produce λ new hosts**
- **Parasitized hosts each produce *c* parasitoids**
- **The probability of a host <u>not</u> being parasitized is $\phi = \phi(P_t)$**
- **The probability of a host <u>being</u> parasitized is $1 - \phi$**

$$H_{t+1} = \lambda H_t \phi$$

$$P_{t+1} = cH_t(1 - \phi)$$

Nicholson-Bailey Model - derivation

What is ϕ?

- **Parasitoids oviposit randomly into hosts, even if host is already parasitized**

- **each host is attacked at a rate aP_t , where *a* is parasitoid's search efficiency**

Nicholson-Bailey Model - derivation

What is ϕ?

- **Parasitoids oviposit randomly into hosts, even if host is already parasitized**

- **each host is attacked at a rate aP_t , where *a* is parasitoid's search efficiency**

- **Number of times a host is attacked over a year is described by the Poisson distribution:**

probability (attacked *n* times) $= \dfrac{(aP_t)^n e^{-aP_t}}{n!}$

ϕ = **probability (attacked 0 times)**

$= e^{-aP_t}$

Nicholson-Bailey Model - derivation

Substitute ϕ into equations for host and parasitoid densities in year t+1:

$$H_{t+1} = \lambda H_t e^{-aP_t}$$

$$P_{t+1} = cH_t\left(1 - e^{-aP_t}\right)$$

λ = no. of new hosts produced by one unparasitized host
= e^r , where *r* is intrinsic growth rate
a **= parasitoid searching efficiency**
c **= no. of new parasitoids produced by a parasitized host**

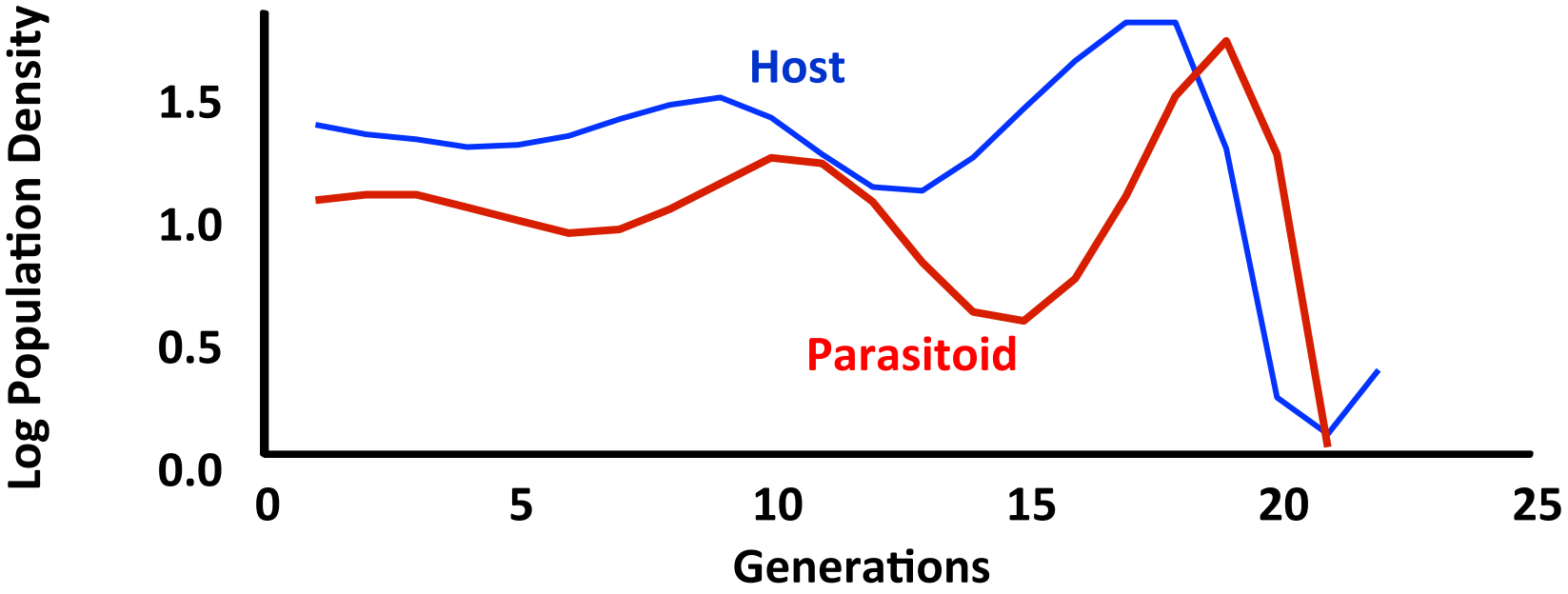
Nicholson-Bailey Model - dynamics

- **Recall Lotka-Volterra model: density-independent prey growth and random predator-prey encounters (Type I response) led to neutral stability and cycles**

- **N-B model makes same assumptions, but there is a delay: population sizes in year t+1 determined by populations in previous year**

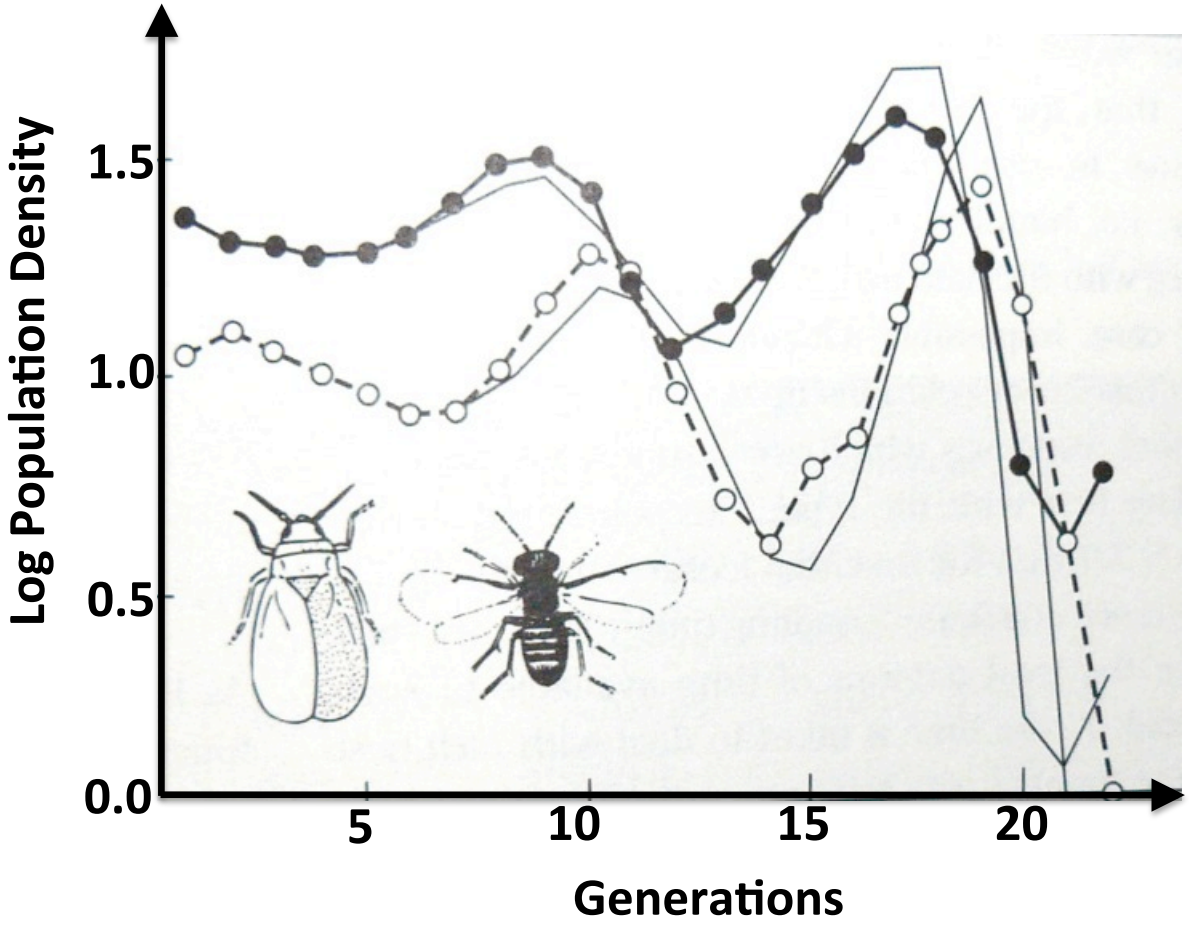
… so what type of dynamics do you expect from the N-B model? (i.e. are delays stabilizing or destabilizing?)

Nicholson-Bailey Model - dynamics



Cycles of increasing amplitude, leading to <u>extinction</u>

Whitefly-chalcid interaction



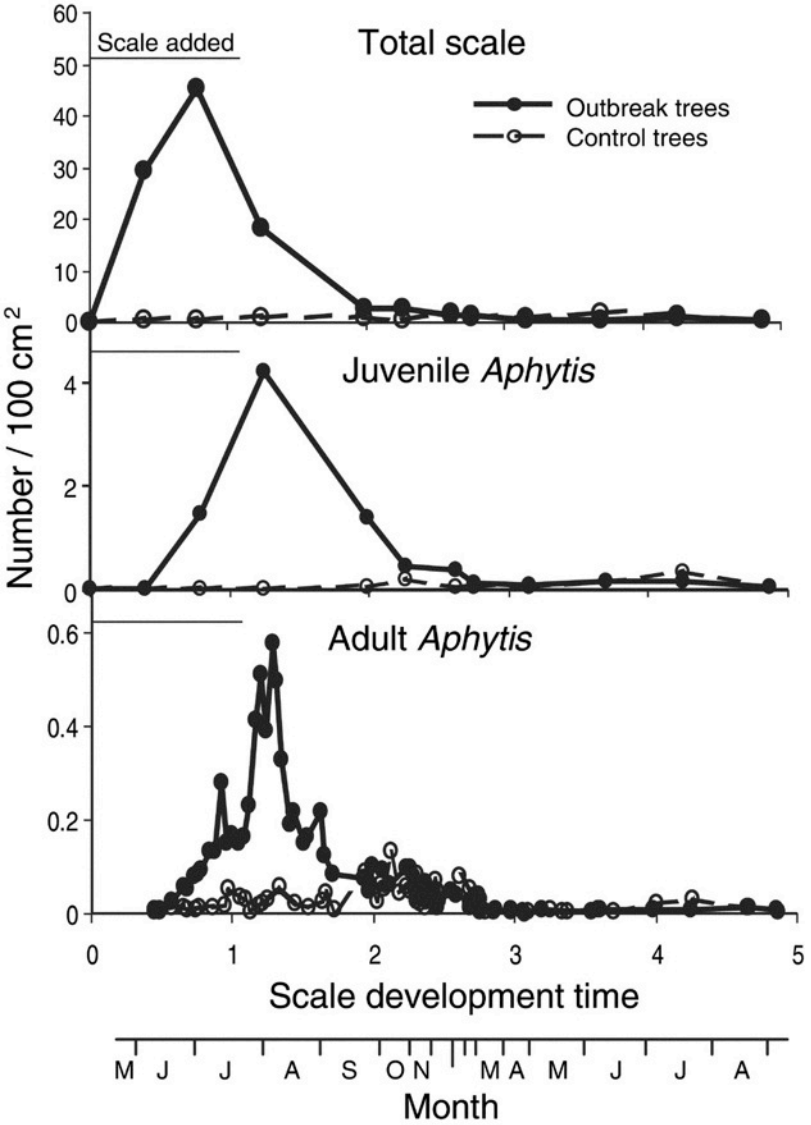
● greenhouse whitefly (*Trialeurodes vaporariorum*)

○ chalcid (*Encarsia formosa*)

— fitted N-B model

Nicholson-Bailey model captures dynamics of simple lab population

BUT red scale-*Aphytis* populations persisted!



There must be some stabilizing process not accounted for in the basic N-B model

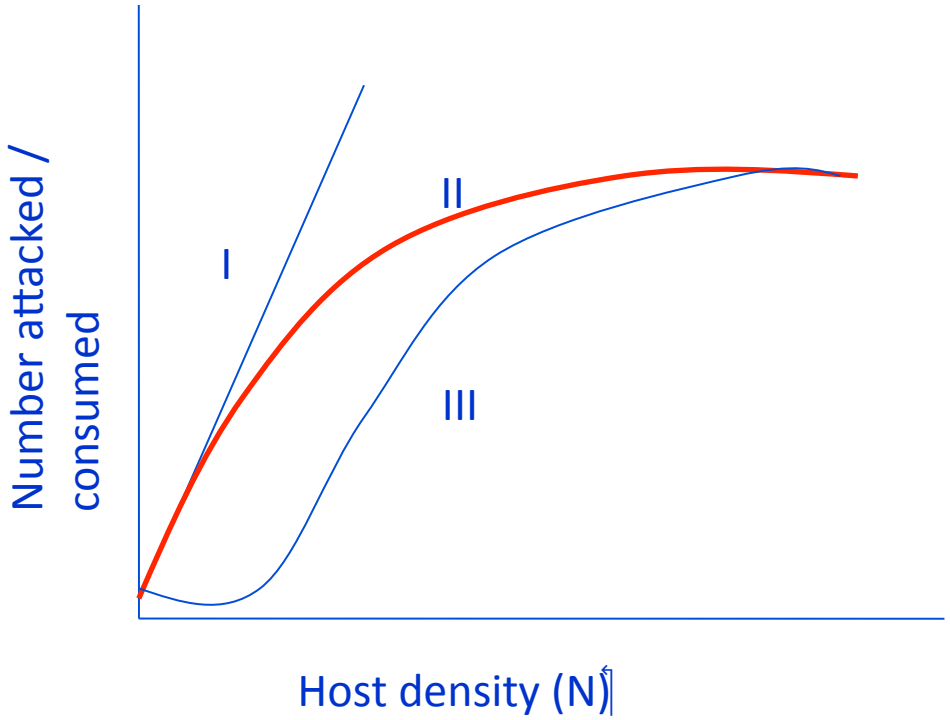
2 min break: think of some potentially stabilizing mechanisms (allowing long-term coexistence)

Adding more biological realism

Think back to predator-prey dynamics

We added a saturating (Type II) functional response to describe handling time and predator satiation

Was this stabilizing?



Adding more biological realism

Think back to predator-prey dynamics

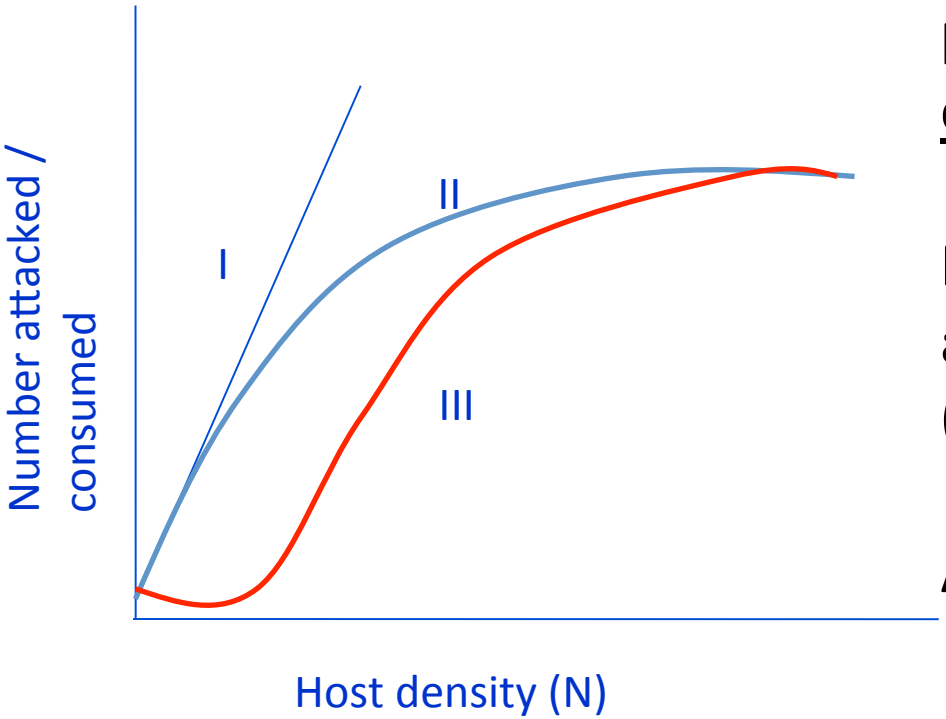
We added a saturating (Type II) functional response to describe handling time and predator satiation

Was this stabilizing?

NO! Unstable cycles. Predator saturation acts like a delay (delays are destabilizing)

Other stabilizing mechanisms

Host switching (Type III functional response)



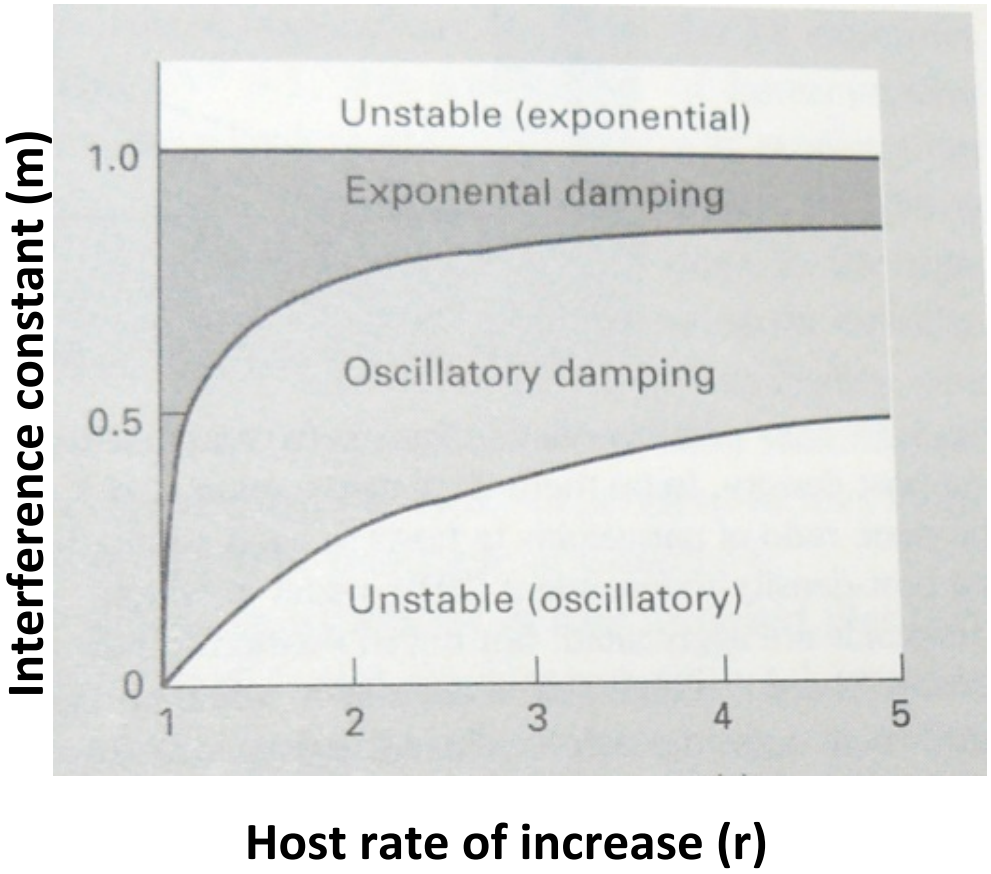
If parasitoid is a generalist, its population stays roughly constant

Number of hosts attacked has a Type III functional response (sigmoid)

Again, hosts escape when rare

Other stabilizing mechanisms

Parasitoid self-regulation (interference competition for hosts)



Females avoid ovipositing in hosts already parasitized

Replace $\phi = e^{-aP_t}$ **with**

$$\phi = e^{-aP_t^{1-m}}$$

***m*=interference coefficient**

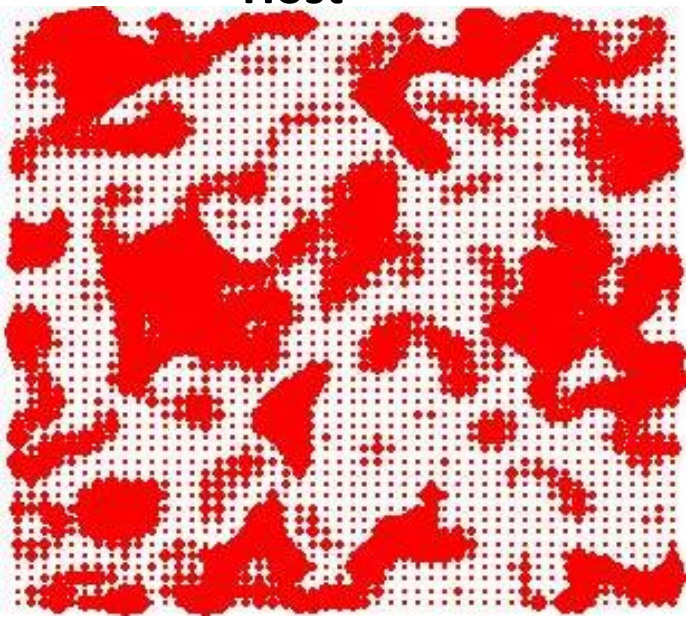
Stabilizing for *m* close to 1 (reduced parasitoid efficiency)

Other stabilizing mechanisms

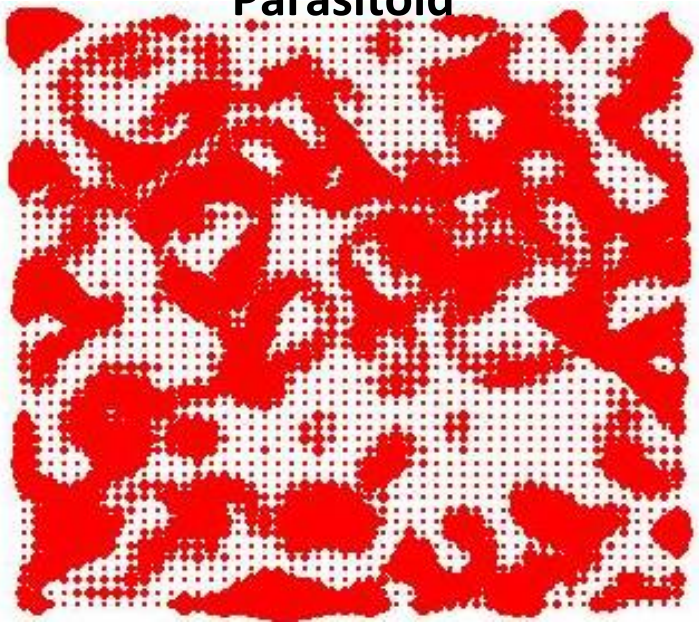
Spatial heterogeneity

- Within-patch dynamics given by basic N-B model (unstable)
- Patches coupled by host and parasitoid dispersal
- Asynchronous fluctuations in patches allow metapopulation persistence

Host



Parasitoid



Summary – so far

Parasitoids are a ubiquitous natural enemy of insects

Since generations are non-overlapping, delays lead to inherent instability (Nicholson-Bailey)

Including prey self-regulation is stabilizing, but more complex dynamics possible (hence variable success of parasitoids as biocontrol)

Factors reducing the parasitoid's search efficiency also tend to be stabilizing

Adding more biological realism

What about host self-regulation (host carrying capacity)?

Is this generally a stabilizing or destabilizing force?

Adding more biological realism

What about host self-regulation (host carrying capacity)?

Is this generally a stabilizing or destabilizing force?

Intraspecific density dependence is stabilizing

- **true for competition models (-/-): coexistence when intraspecific comp stronger than interspecific comp**

- **also true for predator-prey (-/+) dynamics: cycles of L-V model disappear with density-dependent prey growth**

N-B model with host self-regulation

Step 1: Original N-B model

$$H_{t+1} = \lambda H_t e^{-aP_t}$$

$$P_{t+1} = cH_t\left(1 - e^{-aP_t}\right)$$

recall $\lambda = e^r$ **is the host growth rate**

$$H_{t+1} = e^r H_t e^{-aP_t}$$

$$P_{t+1} = cH_t\left(1 - e^{-aP_t}\right)$$

$$H_{t+1} = H_t e^{r-aP_t}$$

$$P_{t+1} = cH_t\left(1 - e^{-aP_t}\right)$$

N-B model with host self-regulation

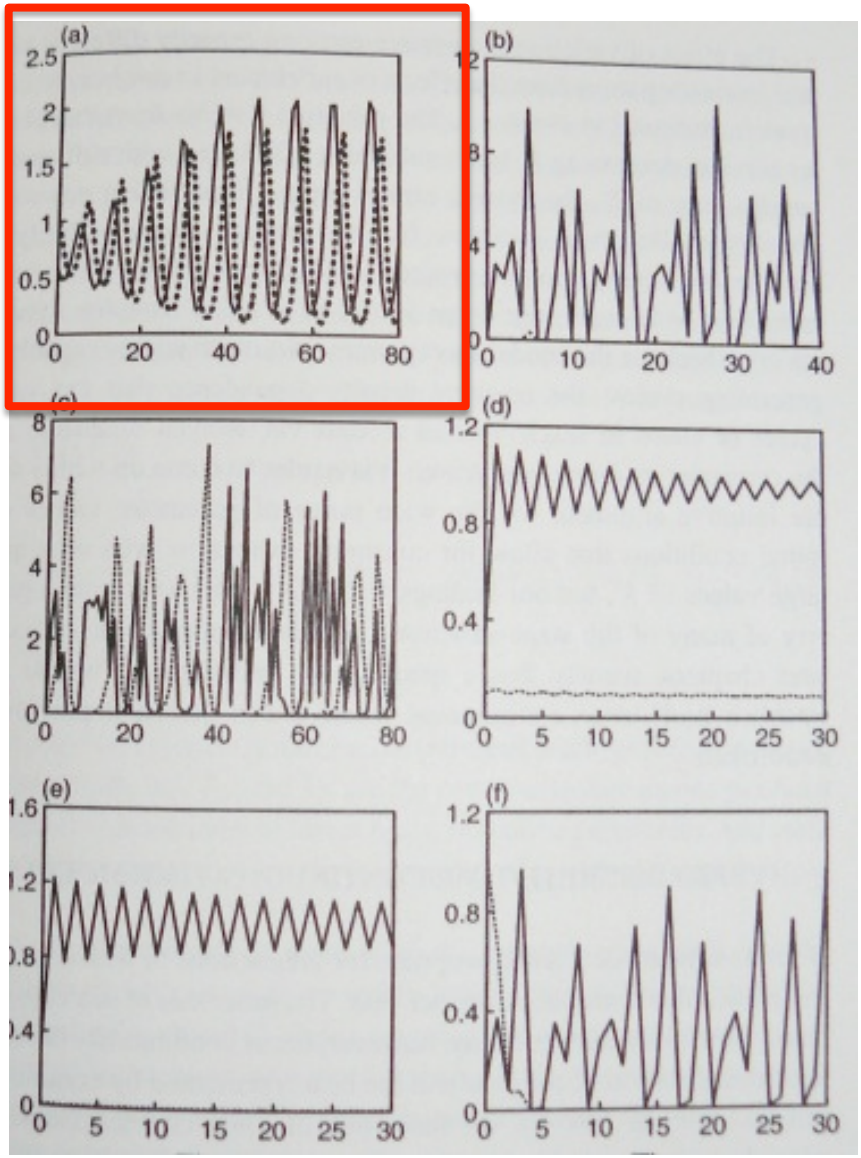
Step 2: Add density dependence (r➔r-rH/K):

$$H_{t+1} = H_t e^{r - rH_t / K - aP_t}$$

$$P_{t+1} = cH_t \left(1 - e^{-aP_t}\right)$$

K **is the prey carrying capacity**

N-B model with host self-regulation

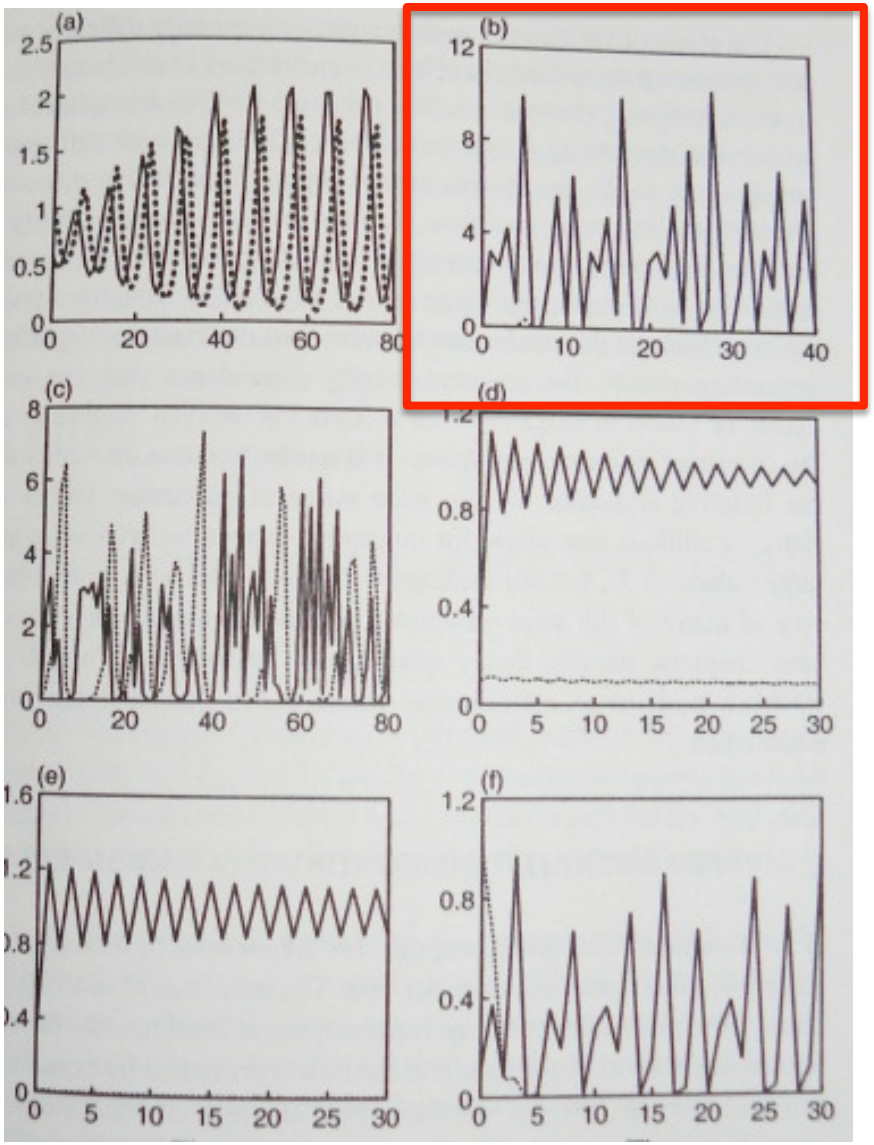


Variety of outcomes possible:

(a) Host and parasitoid persist in stable limit cycle (r=1,K=3)

Interaction of density dependence (stabilizing) and lags (destabilizing)

N-B model with host self-regulation

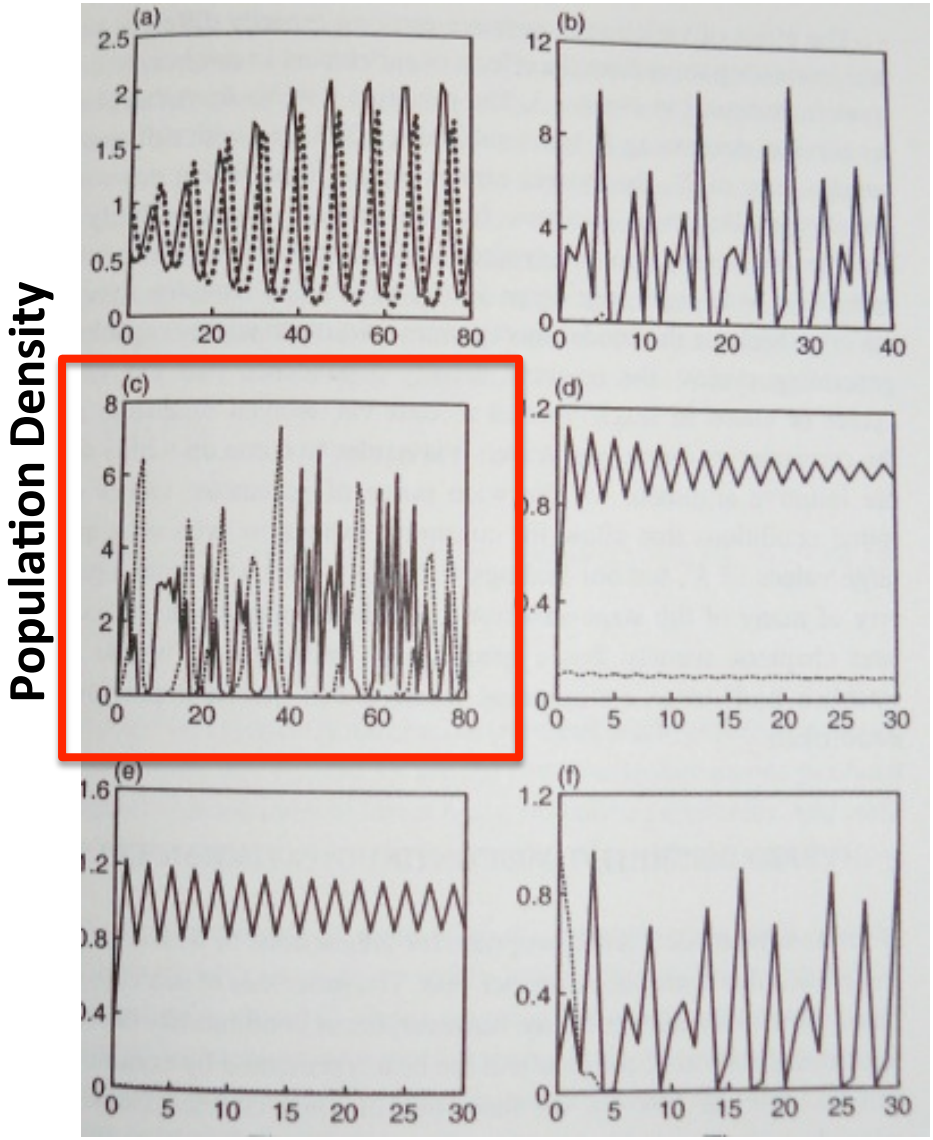


(b) Parasitoid extinction, host cycles (r=3.5,K=3)

Paradox of enrichment

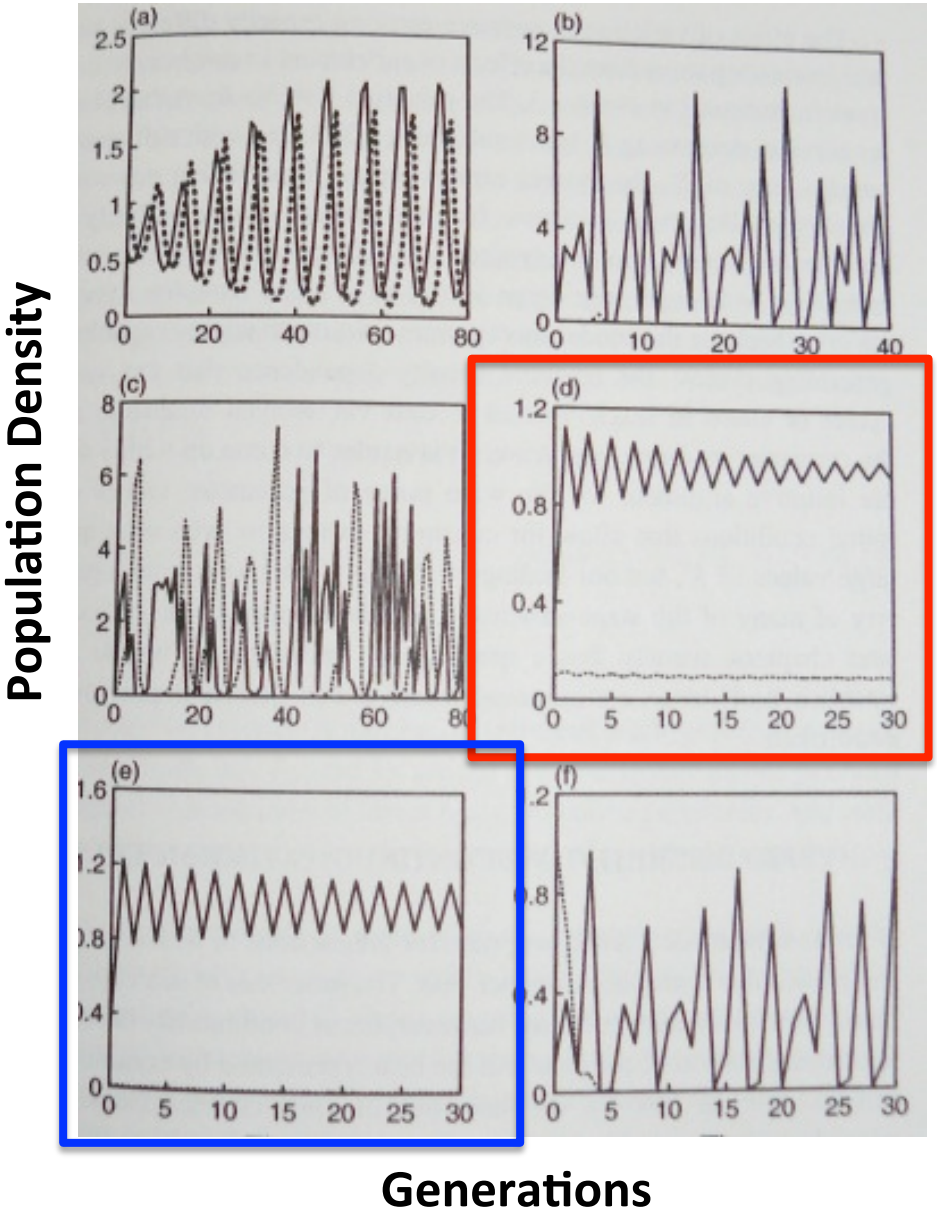
(consumer cannot persist when resource production is higher)

N-B model with host self-regulation



(c) Host and parasitoid persist in an unpredictable manner: chaos! (r=3,K=3)

N-B model with host self-regulation



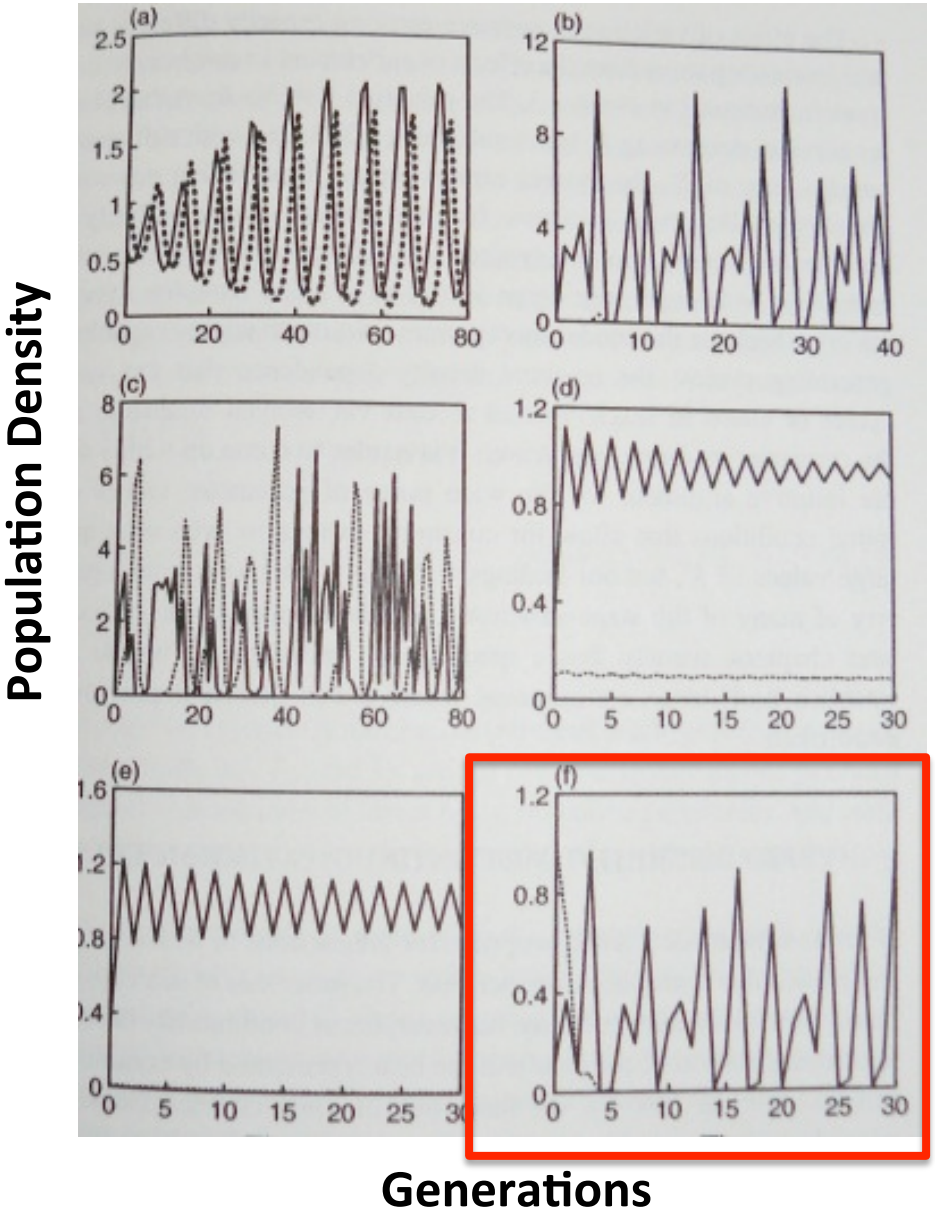
Alternative stable states:
outcome depends on initial conditions (r=2, K=1)

(d) Stable equilibrium of host and parasitoid

(e) Parasitoid extinction, host stable equilibrium

Could explain variable success of biocontrol

N-B model with host self-regulation



Variety of outcomes possible:

(f) Parasitoid extinction
(r=3.5,K=0.3)

Strong self-regulation in the host (low K)

N-B model with prey self-regulation

In summary:

Host density dependence can promote stable coexistence, at an equilibrium or limit cycle, but more complex dynamics possible (typical of nonlinear, discrete models)

Analogies to predator-prey dynamics

- **K too low, parasitoid unable to persist**
- **Moderate K, stable equilibrium**
- **Increasing K leads to cycles (paradox of enrichment)**
- **High K causes extinction of one or both species (like basic N-B model, instability 'wins')**

California red scale revisited

- Murdoch et al. (2005) used decades of field and laboratory studies to parameterize a detailed model of the host-parasitoid interaction

- details of the host and parasitoid life-history determined stability:

1. invulnerable adult stage
2. Rapid parasitoid development

```
m<-seq(0,1,0.01)

plot(m,exp(-10^(1-m)),type="l",xlab="Interference coefficient,m",ylab=expression(paste("Prob. escaping parasitoids, ",phi)))
```