

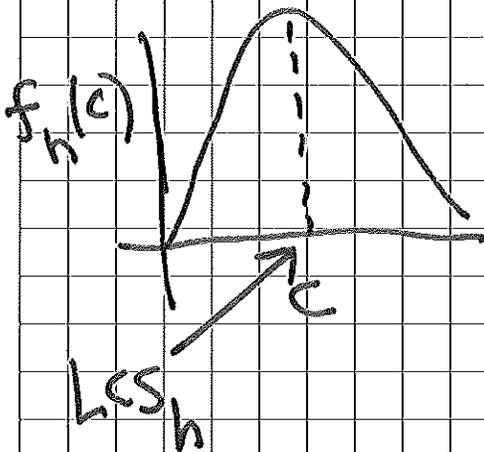
A Bit More Intuition

$$F(x,t) = \left(1 - \sum_h \lambda_h\right) e^{-\mu_s} F(x,t) + \sum_h \lambda_h \max_{c \leq x} \left[f_h(c) + e^{-\mu_s - \mu_d t} F(x-c, t+1) \right]$$

$$+ \sum_h \lambda_h \max_{c \leq x} \left[f_h(c) + e^{-\mu_s - \mu_d t} F(x-c, t+1) \right]$$

$$\Downarrow$$

$$c^*(x, h, t)$$

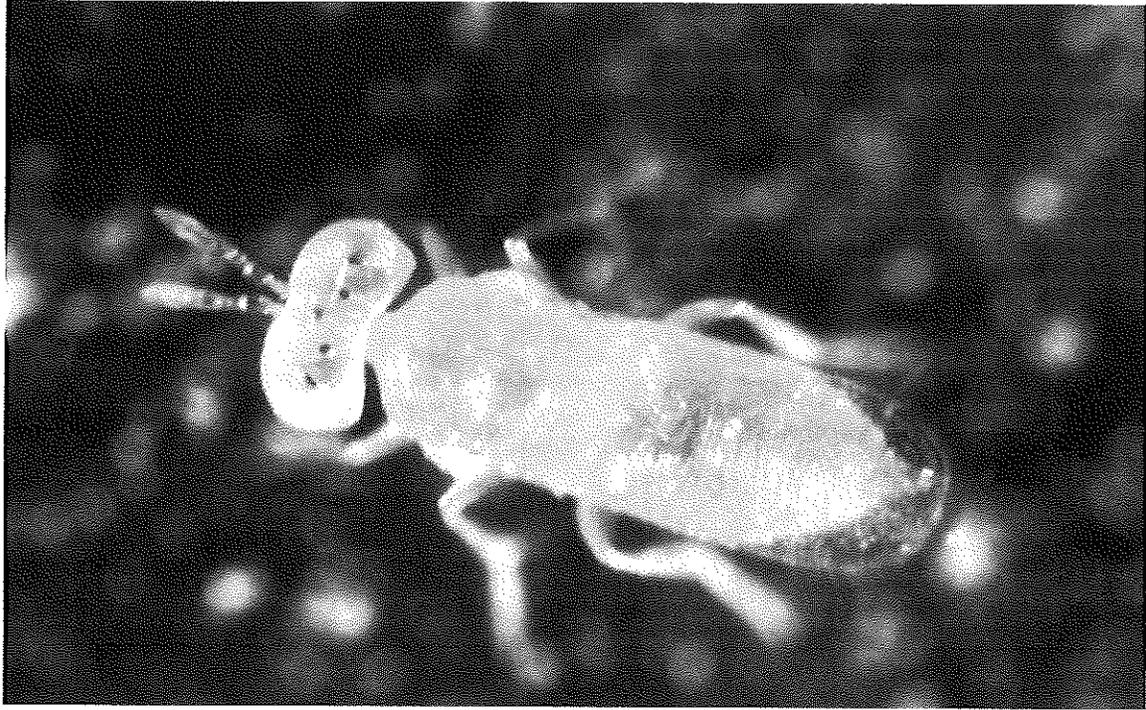


As t increases we predict

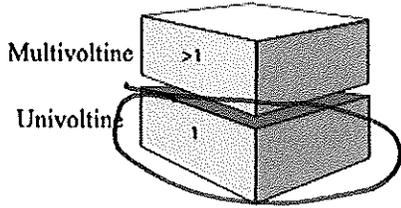
- Clutches increase
- Clutches never exceed LCS_h

At $t=1$, we predict

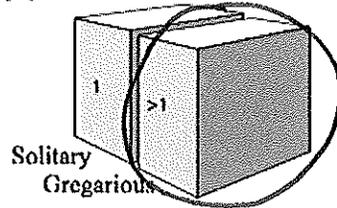
- Smallest clutches she lays
- The clutches will increase with egg complement



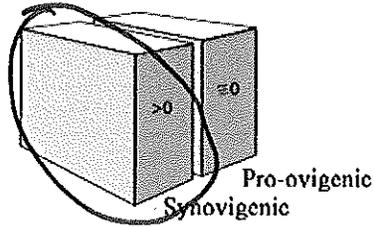
a) Generations per Year:



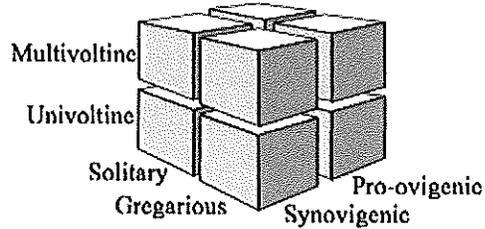
b) Eggs per Host:



c) Egg Production After Emergence:



d) Combining the characteristics:



Some aphid parasitoids are synovigenic
 When encountering a host they may
 host-feed

Parasitoids need carbohydrates to run the operation

$X(t)$ = current egg complement

$R(t)$ = current level of reserves for
 making eggs

$G(t)$ = current level of glucose

Dynamics

x, $X(t+1) = X(t) - \text{clutch} + 1$

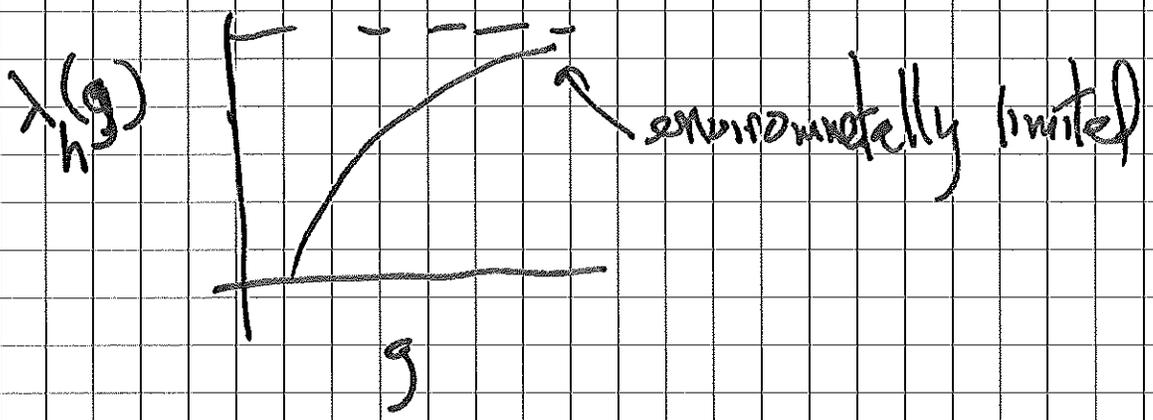
← Assuming every period an egg is made (if she can)

r, $R(t+1) = R(t) - \alpha_e + Y_h$

↑ resource cost of making an egg
← increase in resources if she feeds on a host of type h

g, $G(t+1) = G(t) - \alpha_g + Y_g$

→ metabolic cost of living up period
↑ increase in glucose if she goes to a nectar source



$$F(x, r, g, t) = \max E \left\{ \begin{array}{l} \text{fitness accumulated} \\ \text{through ovipositions} \\ \text{between } t \text{ and } T \end{array} \right\}$$

$$\left. \begin{array}{l} \downarrow \\ x(t) = x, r(t) = r, g(t) = g \end{array} \right\}$$

$$F(x, r, g, T) = 0$$

$$F(x, r, g, t) = \max \left[\begin{array}{l} V_{\text{host}}(x, r, g, t); \\ V_{\text{nectar}}(x, r, g, t) \end{array} \right]$$

fitness value of
seeking hosts from
 (x, r, g) at time
 t

fitness value of
seeking glucose
from (x, r, g)
at time t

Fitness value of seeking nectar

22.18

z

$$I_z = \begin{cases} 1 & \text{if } z > 0 \\ 0 & \text{o.w.} \end{cases}$$

$$V_{\text{nectar}}(x, r, g, t)$$



$$\leftarrow \lambda_{\text{nectar}}(g) e^{-m_s} F(x+1, I_{r-\alpha_e})$$

$$(r-\alpha_e) \cdot I_{r-\alpha_e} + r(1 - I_{r-\alpha_e}),$$

$$g - \alpha g + \gamma g, t+1)$$

$$+ (1 - \lambda_{\text{nectar}}(g)) e^{-m_s} F(x, I_{r-\alpha_e})$$

$$(r-\alpha_e) I_{r-\alpha_e} + r(1 - I_{r-\alpha_e}),$$

$$g - \alpha g, t+1)$$

22.19

$$V_{\text{host}}(x, r, g, t)$$

$$= \left(1 - \sum_h \lambda_h(g)\right) e^{-m_s} F(x + I_{r-\alpha_e})$$

$$(r - \alpha_e) I_{r-\alpha_e} + r(1 - I_{r-\alpha_e}),$$

$$g - \alpha_g, t+1)$$

$$+ \sum_h \lambda_h \max \left[V_{\text{feed}}(x, r, g, t); V_{\text{ovip}}(x, r, g, t) \right]$$

$$V_{\text{feed}}(x, r, g, t) = e^{-m_s - m_f \tau_f}$$

$$F(x + I_{r-\alpha_e})$$

$$(r - \alpha_e) I_{r-\alpha_e} + r(1 - I_{r-\alpha_e}) + \lambda_h,$$

$$g - \alpha_g - \alpha_g, t+1 + \tau_f)$$

22.20

$$V_{ovip}(x, r, g, h, t)$$

$$= \max_{c \in X} \left[f_h(c) \right.$$

$$\left. + e^{-m_s - m_0 t} F(x - c + I_{r-\alpha_e}) \right.$$

$$\left. \begin{aligned} & (r - \alpha_e) I_{r-\alpha_e} + r(1 - I_{r-\alpha_e}), \\ & g - \alpha_{ovip} - \alpha_g, t + 1 + \gamma \end{aligned} \right]$$

Clark and Mangel 2000

Ch 4

29 April

AMS 215: Important Dates and Deadlines. Revised

May 3 (noon): Paper you like #3 in dropbox folder, report to Marc

May 8 (midnight): Problems 6, 7 due

May 10 (noon): Paper you like #4 in dropbox folder, report to Marc

May 13: In class discussion of your projects (Vanessa, moderator).

May 15: No class (coding day)

May 17: Description of your project to Marc (midnight).

May 22: No class (coding day)

June 13 (midnight): Project reports/problems due

"It is in the heap of the data not
the heap of the data - as
Muhammad Ali might say -
that insight is gained"

Alan Gopnik
Amigos and Ages

Bayes's Theorem

$$P(A|B) = \frac{P(B|A)P(A)}{P(B)}$$

Assessing the Fitness of Sub-optimal Strategies

$$i^*(x, t)$$

$j(x, t) \sim$ some other strategy

~~Relative cost~~

$$c(x, j, t) = \frac{V(i^*(x, t), x, t) - V(j, x, t)}{V(i^*(x, t), x, t)}$$



Relative cost of following strategy j rather than $i^*(x, t)$ when $X(t) = x$

29.2

THE COMMON CURRENCY FOR BEHAVIORAL DECISIONS

JOHN M. McNAMARA AND ALASDAIR I. HOUSTON*

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Submitted September 18, 1984; Accepted July 30, 1985

This is the very coinage of your brain. (Shakespeare, *Hamlet*, III, iv, 137)

Any attempt to understand behavior in terms of the evolutionary advantage that it might confer has to find a "common currency" (McFarland and Sibly 1975; McCleery 1978) for comparing the costs and benefits of various alternative courses of action. For example, an animal might have to decide among various feeding strategies or between feeding and defending a territory. It is easy to say that such actions should be compared in terms of fitness, but fitness is defined over the whole of an animal's life, and it is not easy to specify the contribution of an individual action to the animal's life history.

Attempts to analyze behavior over a short time interval have often used a very simplified currency. For example, the foraging behavior of many animals has been evaluated in terms of the net rate at which energy is gained (for reviews, see Pyke et al. 1977; Krebs 1978; Krebs et al. 1983). But this currency is inadequate because the value of a food item depends on the animal's state (see Caraco 1980; Stephens 1981; McNamara and Houston 1982; and below).

Another objection to this currency is that it ignores other activities in the animal's repertoire. Even if the animal is not breeding, it must avoid predators. Although some researchers have represented the cost of the time spent scanning for predators as feeding time lost (Pulliam et al. 1982), a more rigorous approach to the problem is desirable. One such approach is to use a cost function that represents both the value of food to the animal and the costs of predation. Optimal behavior minimizes the integral of the cost function over a period of time. This sort of framework was pioneered by McFarland (e.g., McFarland 1971, 1976, 1977; Sibly and McFarland 1976) and reviewed by McFarland and Houston (1981). In the context of predation risk, it has been used to account for the effect of a kingfisher on the foraging behavior of sticklebacks (Milinski and Heller 1978; Heller and Milinski 1979). Major concerns about this approach are the somewhat arbitrary nature of the cost function and the strong suspicion that different cost

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To assess the expected cost of the suboptimal trajectory:

- ① Pick the strategy $j(x, t)$
- ② Simulate forward to get

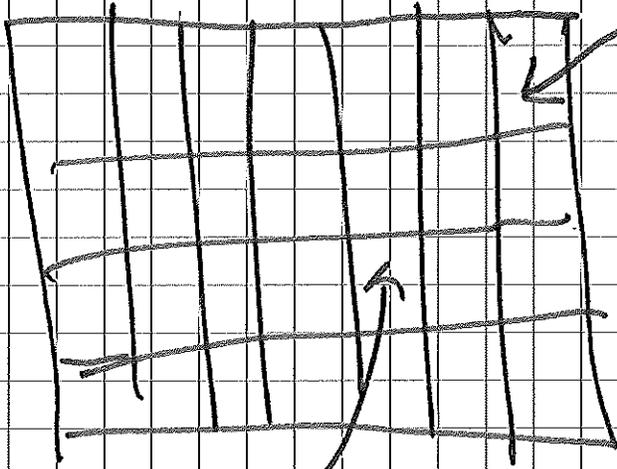
$p(x, t)$ = Fraction of times that the simulated organisms are in state x at time t

③ make

$$\bar{C}(j) = \sum_t \sum_x p(x, t) C(x, j, t)$$

Spatial Ecology

(29, 11)



$$i = (i_1, i_2)$$

x-coord
longitude

y-coord
latitude

$$j = (j_1, j_2)$$

$X(t)$ = resource at time t

$L(t)$ = location at time t

Y_i = gain of successful
when foraging in
patch i

λ_i = prob find food in patch i

a_{ij} = energetic cost of going
from patch i to patch j

$x=1$

$x=2$

$x=3$

$x=4$

t_{ij} = travel time between patch
i and j plus one unit
of foraging time in patch j
($t_{ii} = 1$)

29.5

M_{ij} = rate of mortality for all this
travel

m_j = rate of mortality when foraging
for 1 period in patch j

$F(x, i, t) = \max E \{ \text{Terminal pay-off} \}$

$X(t) = x, L(t) = i$

$\Phi_i(x) = \text{Future expected reproductive success}$
given ~~$X(0) = x$~~ $X(T) = x, L(T) = i$

End Condition

$$F(x, i, T) = \Phi_i(x)$$

$$\begin{aligned} \dot{m}_i &= 0 \\ m_i &> 0 \\ t_{ii} &= 1 \end{aligned}$$

$$F(x, i, t) = \max_j \left\{ e^{-m_{ij} t_{ij} - m_j} \lambda_j F(x - \alpha_{ij} + \gamma_j, \overset{j}{t_{ij}}, t + t_{ij}) \right.$$

all the places
to possibly
visit

$$\left. + (1 - \lambda_j) F(x - \alpha_{ij}, j, t + t_{ij}) \right\}$$

Loop Over Time (t)

Loop Over State (s)

Loop Over ^{ALL} Current Locations (i)

Compute the fitness value of going to each possible location and pick the max.

$$V(x, i, j, t)$$

$$= e^{-m_j t_{ij} - m_j} \left\{ \lambda_j F(x - \alpha_{ij} + Y_j, j, t + t_{ij}) + (1 - \lambda_j) F(x - \alpha_{ij}, j, t + t_{ij}) \right\}$$

$$F(x, i, t) = \max_j V(x, i, j, t)$$

^So easy!
J. Smith

Notation

\in means within the set

$j \in J_s(i) \Rightarrow$ all the cells j that can be visited from cell i in one period

~~$$V_s(x, i, t) = \max_{j \in J_s(i)}$$~~

$$F(x, i, t) = \max E \{ \text{terminal pay off} \mid x(t) = x, L(t) = i \}$$

$$= \max [V_s(x, i, t), V_b(x, i, t)]$$

fitness value if search mode is used

fitness value if transit mode is used

29.10

$$V_s(x, i, t) = \max_{j \in J_s(i)} e^{-m_{ij} - m_j} \left[\lambda_s^{(j)} F(x - \alpha_{ij} + V_{ij}, j, t+1) + (1 - \lambda_s^{(j)}) F(x - \alpha_{ij}, j, t+1) \right]$$

Transit Mode

$J_b(i)$ = collection of cells that
could be reached from cell
 i in one period when in
transit mode

For each j here

$K(j)$ = collection of cells visited on the
way to cell j from cell i

let $k_1, k_2, k_3 \dots$ in $K(j)$

first all transit through

second all transit through

$$\begin{aligned}
 V_b(x, i, t) = \max_{j \in J_b(i)} & \left[e^{-m_i k_1 - n_{k_1}} \lambda_b(k_1) \right. \\
 & F(x - \alpha_i k_1 + Y_{k_1}, k_1, t+1) \\
 & + (1 - \lambda_b(k_1)) e^{-m_i k_1 - n_{k_1}} \\
 & \left. \lambda_b(k_2) F(x - \alpha_i k_2 + Y_{k_2}, k_2, t+1) \right. \\
 & + (1 - \lambda_b(k_1))(1 - \lambda_b(k_2)) e^{-m_i k_1 - m_{k_1 k_2} - n_{k_2 k_3} - m_{k_3}} \\
 & \left. \lambda_b(k_3) F(x - \alpha_i k_3 + Y_{k_3}, k_3, t+1) \right. \\
 & + \dots \text{ (you see how the logic goes)}
 \end{aligned}$$

29.12

An alternative way

$\lambda_s(j), \lambda_b(j)$ as before

$\lambda_s > \lambda_b$

$t_{ij}(s)$

$> t_{ij}(b)$

$t_{ij}(s) \sim$ travel time between cell i and j when in searching mode

$t_{ij}(b) \sim$ " " " " " "

" " " transit node

$J(i) \sim$ cells adjacent to cell i

$$F(x, i, t) = \max [V_s(x, i, t), V_b(x, i, t)]$$

$$V_s(x, i, t) = \max_{j \in J(i)} e^{-m_{ij} t_{ij}(s) - m_j}$$

$$\lambda_s(j) F(x - \alpha_{ij} + V_j, t + t_{ij}(s))$$

$$+ (1 - \lambda_s(j)) F(x - \alpha_{ij}, t + t_{ij}(s))$$

$$V_b(x, i, t) = \max_{j \in J(i)} e^{-m_{ij} t_{ij}(b) - m_j} \quad 29.13$$

$$\left[\lambda_b(j) F(x - \alpha_{ij} + Y_{ij}, j, t + t_{ij}(b)) \right]$$

$$+ (1 - \lambda_b(j)) F(x - \alpha_{ij}, j, t + t_{ij}(b)) \left. \right]$$

Page 1

Increasing Fidelity to Nature

~~Time-dependent parameters~~

~~State dependence to parameters (e.g. size dependent predation)~~

~~Variable handling and/or travel times~~

~~Per period reproduction~~

~~Needing to forage for multiple nutrients (e.g. sources of carbohydrate, sources of protein — like that mosquito which experienced a mortality event during lecture on 3 April 2013)~~

~~Anthropogenic mortality (Problem 5)~~

~~Visiting multiple patches before returning home~~

~~Spatial structure and networks of patches~~

~~Disease (both $\beta_1 > 0$ and disease causes α or β to increase or λ to decline)~~

Dependent young

Learning

Age structure (affecting foraging ability, and perhaps predator avoidance)

Patch depletion

Schooling behavior

Games against conspecifics

Predator-prey games

1.2
AL*

Presenting Your Project Verbally and In Writing

You can use the same structure for sharing your project with your colleagues on May 13 (up to the Results section) and with me in your write up. What follows is intended to be helpful guidance, so that if you think you need to deviate from it, that is okay.

Scientific Question

Explain the scientific question that motivates you. Do this as if you were at a party and somebody - not an expert - asked "What do you do and why?"

State Variables

Explain what the state variable(s) is/are and why you picked them.

Remember: simple is better at the start.

Remember: simple is better at the start.

Dynamics of the State Variables

Explain how the state variable(s) change(s) in time.

Components of the Environment

What components of the environment are you modeling (e.g. in the Basic Patch Selection Problem they are the rate of mortality, probability of finding food, and cost of foraging in each patch).

Fitness

What metric of fitness are you using? Is it only terminal fitness or does it also involve a per-period increment. Only now should you define your fitness function.

Dynamic Programming Equation

What SDP equation are you going to/did you solve?

----- That's it for the presentation -----

Results

What interesting results have you discovered? Are some of them non-intuitive? This is the meat of your document. Be very thoughtful about showing tables and remember that you should make roughly 5-10 figures for every one you show me.

Discussion

Bring the results back to the scientific question.

Appendix: Pseudocode

Please include a pseudocode (not real code) in your write up. Indicate any places where you used interpolation and how you did it.

-

Tracy May 7: 2-430 NWFs less off site

1
10.2

Disease Ecology

More or less same patch structure $\alpha_i, \gamma_i, \mu_i$ as before

$$\lambda_s(i) = p_i \{ \text{find food in a visit to patch } i \}$$

$$\lambda_s(i, t) = p_i \{ \text{getting sick ~~also~~ from a visit to patch } i \text{ in period } t \}$$

Disease

- Is not fatal
- Sickness could \uparrow mortality or \downarrow finding food
- Illness lasts τ_R days

$$F_h(x, t) = \max E \left\{ \Phi(X(T)) \mid X(t) = x, \text{ healthy at the start of period } t \right\}$$

$$F_s(x, \tau, t) = \max E \left\{ \Phi(X(T)) \mid X(\tau) = x \text{ and have been sick for } \tau (< \tau_R) \text{ days at the start of period } t \right\}$$

$$F_h(x, T) = \Phi(X(T))$$

$$F_s(x, \tau, T) = \Phi(X(T)) \frac{1}{1 + \delta R (\tau_R - \tau)}$$

$R \Leftrightarrow$ reproduction

The SDRs

$$F_h(x, t) = \max_i e^{-\alpha_i} \left[\lambda_f(i) (1 - \lambda_s(i, t)) \right] F_h(x - \alpha_i + Y_i, t+1)$$

"FF" "DGS"

$$+ \lambda_f(i) \lambda_s(i, t) F_s(x - \alpha_i + Y_i, t+1)$$

"FF" "GS"

$$+ (1 - \lambda_f(i)) (1 - \lambda_s(i, t)) F_h(x - \alpha_i, t+1)$$

"DF" "DGS"

$$+ (1 - \lambda_f(i)) \lambda_s(i, t) F_s(x - \alpha_i, t+1)$$

"DF" "GS"

We will use this indicator function

$$I_z = \begin{cases} 0 & \text{if } z > 0 \\ 1 & \text{if } z = 0 \end{cases}$$

$$F_S(x, Y, t) = \max_i e^{-m_i(1+\delta_m)}$$

$$I_{Y_R - (Y+1)} \left[\frac{\lambda_S(i)}{1+\delta_F} F_h(x - \alpha_{i,t} + Y_i, t+1) \right.$$

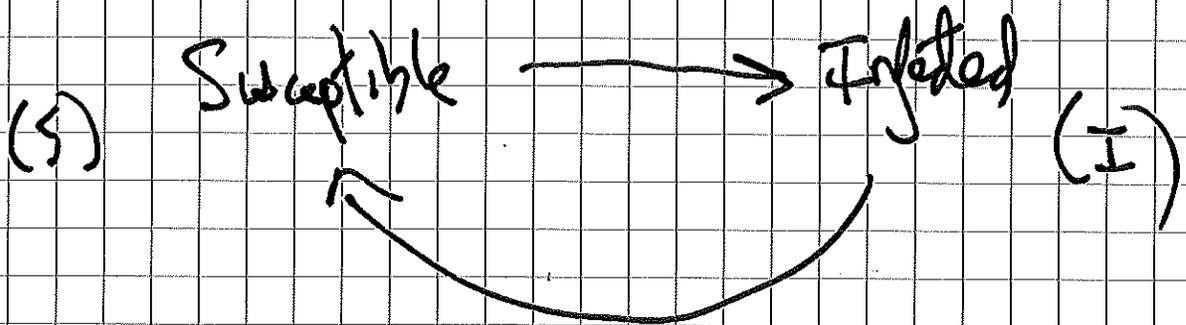
$$\left. + \left(1 - \frac{\lambda_S(i)}{1+\delta_F}\right) F_h(x - \alpha_{i,t}, t+1) \right]$$

$$+ \left(1 - I_{Y_R - (Y+1)}\right) \left[\frac{\lambda_S(i)}{1+\delta_F} F_S(x - \alpha_{i,t} + Y_i, Y+1, t+1) \right.$$

$$\left. + \left(1 - \frac{\lambda_S(i)}{1+\delta_F}\right) F_S(x - \alpha_{i,t}, Y+1, t+1) \right]$$

Finding $\lambda_s(\text{ist})$ for the SIS Model

1.6



$N = \text{size of a closed population}$

$$N = S(t) + I(t)$$

In a small amount of time Δt , ~~the~~ the number of new infections is

$$\beta I(t) S(t) \Delta t + o(\Delta t)$$

$$= \beta I(t) (N - I(t)) \Delta t + o(\Delta t)$$

And the number of infecteds that return to susceptible is

$$\nu I(t) \Delta t + o(\Delta t) \leftarrow \text{Honesty-keeper}$$

"ny" \nearrow

$$I(t+\Delta t) = I(t) + \text{New infections} - \text{Recoveries}$$

$$I(t+\Delta t) = I(t) + \beta I(t)(N-I(t))\Delta t + o(\Delta t) - (\nu I(t)\Delta t + o(\Delta t))$$

$$\frac{I(t+\Delta t) - I(t)}{\Delta t} = \beta I(t)(N-I(t)) + o(\Delta t) - \nu I(t) - o(\Delta t)$$

$$\begin{array}{ccc} \downarrow \Delta t \rightarrow 0 & & \downarrow \Delta t \rightarrow 0 \\ \frac{dI}{dt} & = & \beta I(N-I) - \nu I \end{array}$$

$$\begin{aligned} \frac{dI}{dt} &= \beta I(N-I) - \nu I \\ &= \beta I(t)(N-I(t)) - \nu I(t) \end{aligned}$$

SIS Model

$$\frac{dI}{dt} = \beta I(N-I) - \nu I$$

Steady states

I=0 or

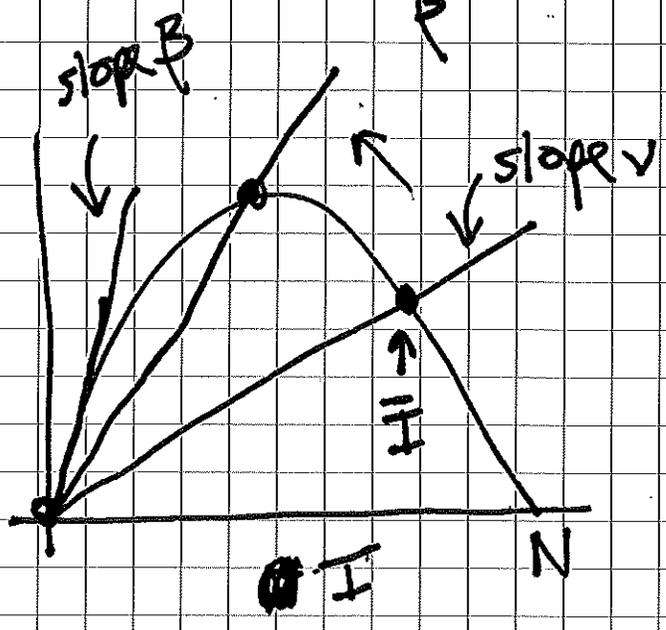
$$\beta I(N-I) = \nu I$$

$$\beta N - \beta I = \nu$$

$$\beta N - \nu = \beta I$$

$$I = \frac{\beta N - \nu}{\beta} = N - \frac{\nu}{\beta}$$

$\beta I(N-I)$
or
 νI



Rate of infections

1.9

$$\beta I(t)(N - I(t))\Delta t + o(\Delta t)$$

Recall from somewhere earlier in the course

$$e^{\beta I(t)(N - I(t))\Delta t}$$

$$= 1 + \beta I(t)(N - I(t))\Delta t$$

$$+ \frac{1}{2} \left[\beta I(t)(N - I(t))\Delta t \right]^2$$

$$+ \frac{1}{6} \left[\beta I(t)(N - I(t))\Delta t \right]^3$$

+ ...

$$e^x = 1 + x + \frac{x^2}{2} + \frac{x^3}{3!} + \frac{x^4}{4!} + \dots$$

so

$$1 - e^{-\beta I(t)(N - I(t))\Delta t}$$

$$= \beta I(t)(N - I(t))\Delta t + o(\Delta t)$$

Why do we like

$$1 - e^{-\beta I(t)(N - I(t)) \Delta t}$$

?

It's like a probability

let's set

$$\lambda_S(i, t) = 1 - e^{-\beta I_i(t)(N - I_i(t)) \Delta t}$$

↑
entire population

so for our single individual

$$\lambda_S(i, t) = 1 - e^{-\beta I_i(t) I_i(t)}$$

The FAB (Forward AND BACKWARD ALGORITHM)

1.11

Step 1 Pick your choice for $\lambda_s(i,t)$
(constant is just fine)

~~Solve the~~ Step 2 Solve the SDPs

Step 3 Do a forward iteration K individuals
(large). Some initially sick, some healthy. Track
 $X_k(t)$, $H_k(t) = 1$ if healthy, 0 if sick
 $u_n^*(X_k(t), t)$
 $u_s^*(X_k(t), T_k, t)$

Step 4 For each patch at each time, compute
using the results in step 3, $I_i(t) = \#$ of
infected individuals in patch i at time t

Step 5 Set $\lambda'_s(i,t) = 1 - e^{-\beta I_i(t)}$

If $\sum_t \sum_i \left(\lambda_s(i,t) - \lambda'_s(i,t) \right)^2$ is

small enough \Rightarrow Miller Time //

Otherwise, replace the $\{\lambda_s(i,t)\}$ by

$\{\lambda'_s(i,t)\}$. Return to Step 2.

6 May 2013

**AMS 215 Project Development Seminar
13 May 2013**

5:00-5:10 Barry
5:10-5:20 Justine
5:20-5:30 Juan
5:30-5:40 Kate E.
5:40-5:50 Elissa
5:50-6:00 Simon
6:00-6:10 Raj
6:10-6:20 Ellen
6:20-6:30 Veronica
6:30-6:40 Rachel
6:40-6:50 Braden
6:50-7:00 Kate R.

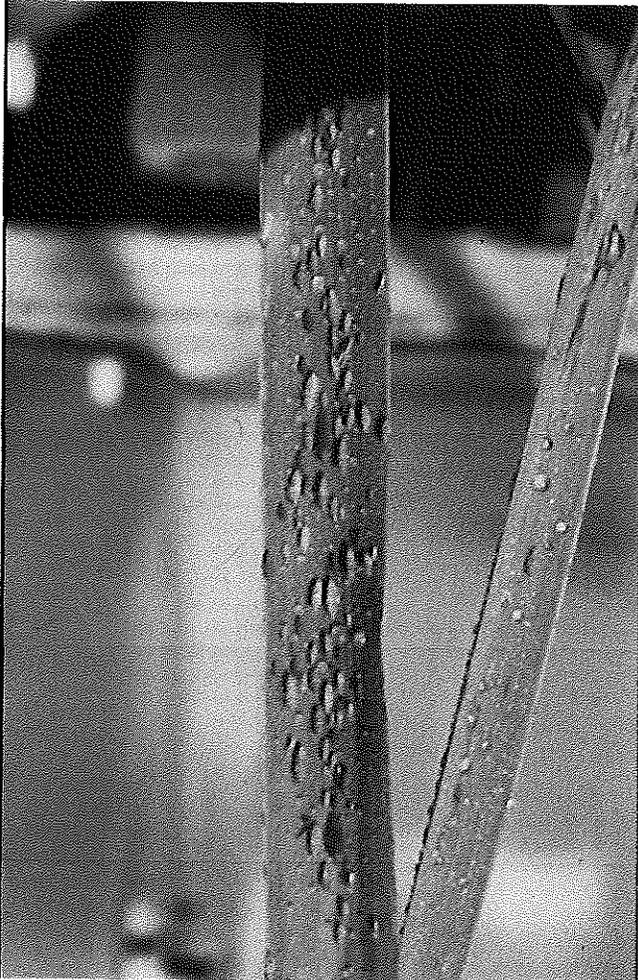
I suggest you plan something like this (writing using the document camera).

Scientific question: 2 minutes
State variables and their dynamics: 3 minutes
Environment: 2 minutes
Measure of fitness: 1 minute
DPE: 1 minute
Questions: 1 minute

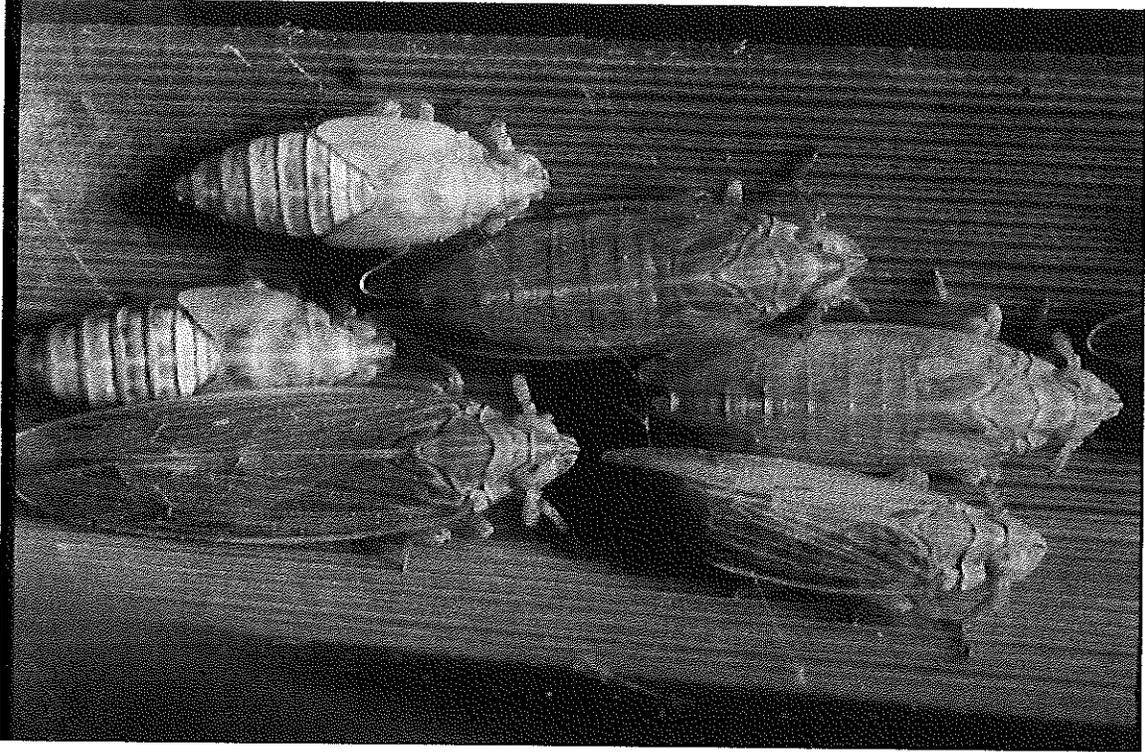
6.1



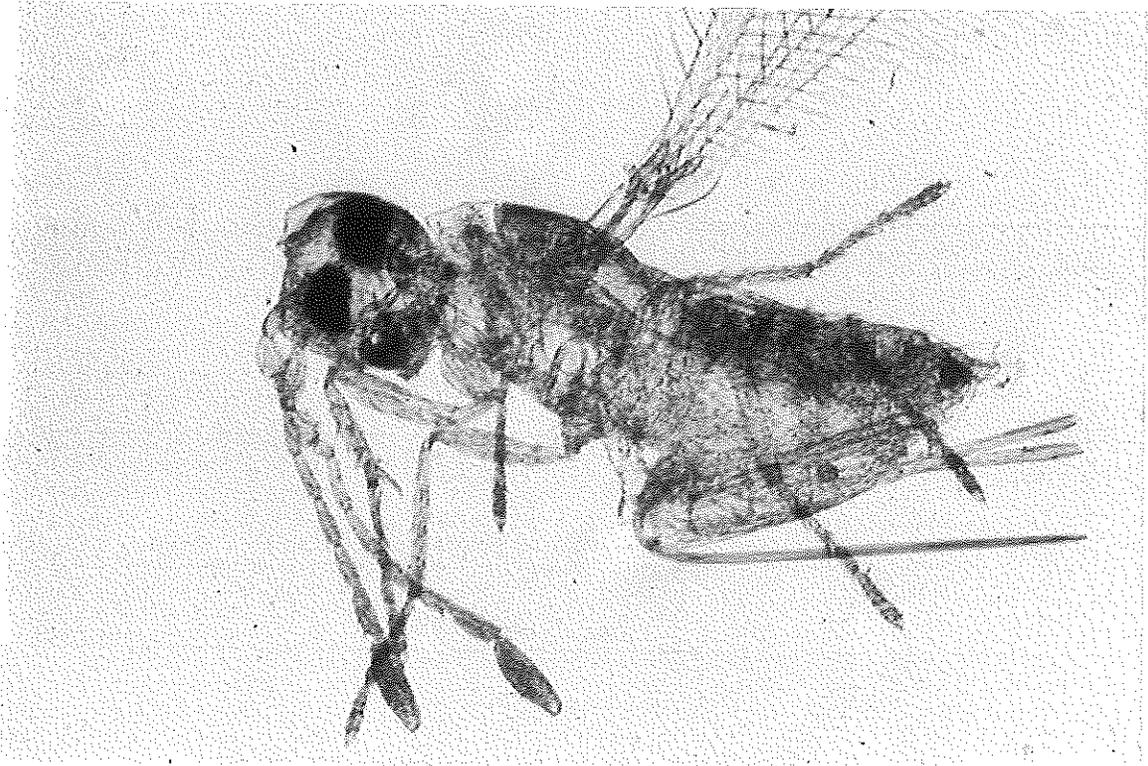
← leafhopper



6.2



Leafhoppers



Anagrus

The link between host density and egg production in a parasitoid insect: comparison between agricultural and natural habitats

Michal Segoli* and Jay A. Rosenheim

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Summary

1. Theory predicts that organisms should invest more heavily in overcoming factors that more frequently emerge as the primary constraints to fitness, and especially, those factors that constrain the fitness of the most highly reproductive members of the population.

2. We tested the hypothesis that the fecundity of a pro-ovigenic parasitoid (where females emerge with their full egg load) should be positively correlated with the mean expectation for oviposition opportunities in the environment. More specifically, we tested whether females from agricultural systems, where hosts are often relatively abundant, emerge with more eggs than those from natural habitats.

3. We studied the pro-ovigenic parasitoid wasp *Anagrus daanei*, which parasitizes eggs of leafhoppers of the genus *Erythroneura*. *Erythroneura* spp. leafhoppers feed on *Vitis* spp. (grapes) and are major pests of commercial vineyards as well as common herbivores of wild *Vitis californica*, which grows in riparian habitats. We sampled leafhoppers and parasitoids from eight vineyards and eight riparian habitats in central California.

4. We found that leafhopper density was higher at vineyards than in riparian habitats, whereas leafhopper egg volume and parasitoid body size did not differ among these habitat types. Parasitoids from vineyards had higher egg loads than parasitoids from wild grapes, and fecundity was positively related to host density across field sites. Parasitoid egg volume was larger in natural sites; however, this variation was not significantly correlated with host density across field sites. Within a single population of parasitoids collected from a vineyard, parasitoid egg load was negatively correlated with longevity, suggesting a trade-off between reproduction and life span.

5. The results may be explained by a rapid evolution of reproductive traits in response to oviposition opportunities; or alternatively, by the occurrence of maternal effects on the fecundity of daughters based on the foraging experience of their mothers.

6. The ability of parasitoid fecundity to track mean host availability is likely to modulate the likelihood that parasitoid fitness will be constrained by a shortage of eggs and strengthen the ability of parasitoids to suppress the population densities of their hosts.

Key-words: fecundity, longevity, egg size, trade-off, *Anagrus*, *Erythroneura*, *Vitis*

Introduction

The lifetime reproductive success of organisms may be limited by many factors such as food availability, mate availability, competition, predation, parasites and pathogens. Organisms can potentially invest in reducing the impact of a particular limiting factor, but the ability to overcome one factor is often traded off against the ability to overcome another (Stearns 1992). Theory predicts that organisms

should invest more heavily in overcoming factors that more frequently emerge as the primary constraints to fitness (Rosenheim, Alon & Shinar 2010). However, this prediction is difficult to test, because the relative importance of different limiting factors may change over the course of an organism's lifetime, and the relative investment in overcoming these factors is often plastic. Moreover, data on the relative importance of factors that limit the reproductive success of organisms in nature are scarce; yet, these are likely to be the factors that shape the evolution of life-history traits.

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$P < 0.001$ for habitat type). Considering only unparasitized leafhopper egg density yielded similar results, but a significant effect of host density was lost if density estimates included only eggs of the preferred leafhopper host.

PARASITOID EGG VOLUME

Residuals of parasitoid egg volume vs. tibia length were larger for riparian habitats compared with vineyards (t -test based on ranks, $T_{1,8} = 1.96$, $P = 0.043$, $n = 6$ for vineyards and 4 for sites with wild grapes). The nonparametric multiple regression also indicated a significant effect of habitat type on mean residual parasitoid egg volume; however, this effect was independent of leafhopper density (Fig. 3, $P = 0.31$ for leafhopper density and $P = 0.05$ for habitat type). Similar results were obtained using the two alternate measures of leafhopper density.

PARASITOID LONGEVITY

Parasitoid longevity was negatively related to egg load (Fig. 4, linear regression, $R^2 = 0.65$, $P < 0.001$, $N = 15$). Despite the small sample size, the results were also significant when considering only females that emerged between 08:00–09:00 h, for which emergence time was determined with certainty ($n = 5$), or only females that emerged before 08:00 h, for which exact emergence time was unknown ($n = 10$).

Discussion

We tested the hypothesis that the fecundity of a pro-ovigenic insect is positively correlated with the mean expectation for oviposition opportunities in the environment in which it was collected. In support of our predictions, parasitoids from agricultural habitats (vineyards), where hosts are more abundant, emerged with more eggs than those from natural riparian habitats (wild grapes), and egg loads were positively associated with host density across field sites. As pro-ovigenic females emerge with their full egg

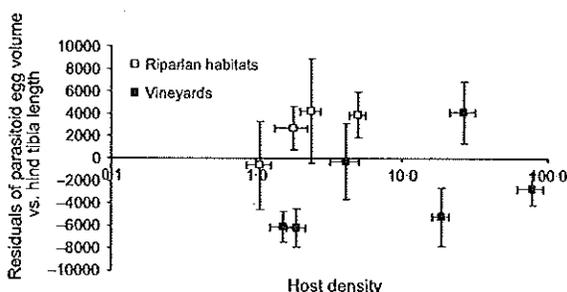


Fig. 3. Residuals of parasitoid egg volume (mean = 25 183 μm³) vs. hind tibia length (μm) in vineyards (solid squares, $n = 6$) and riparian habitats (empty squares, $n = 4$), against host density (on a log scale). Bars represent standard errors of residual egg loads and host density within each field site.

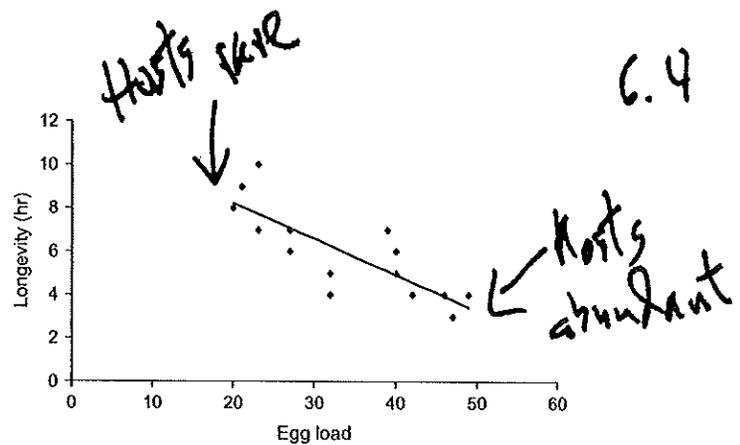


Fig. 4. Relationship between parasitoid egg load and longevity. Linear regression, $N = 19$, $R^2 = 0.38$, $P = 0.009$.

load and do not mature more eggs as adults, this intraspecific variation is not likely to represent a direct plastic response in egg maturation rate to host availability; rather, it is likely to represent an allocation strategy to egg production expressed during parasitoid development inside the host.

Parasitoids traditionally have been considered to be host rather than egg-limited (Godfray 1994). However, a growing body of theoretical and empirical work suggests that the risk of egg limitation is of importance, especially because it is likely to affect the most productive females in the population (i.e. those that had laid many eggs). Hence, parasitoids are probably adapted to balance their investment in overcoming these two opposing risks simultaneously (Heimpel & Rosenheim 1998; Ellers, Sevenster & Driessen 2000; Rosenheim 2011). The link between parasitoid egg load and leafhopper density across field sites documented here may represent an adaptive response to variation in the relative importance of host vs. egg limitation: that is, when oviposition opportunities are plentiful, females are selected to invest more in egg production to reduce the risk of egg limitation, and when oviposition opportunities are scarce, females invest less in egg production and possibly more in survival, to reduce the risk of host limitation. This may suggest a rapid evolution of fecundity and related traits following the recent transition of the host–parasitoid complex from natural to agricultural systems that began around 200 years ago with the establishment of commercial grape production (Doutt & Nakata 1973).

Alternatively, egg loads of parasitoids may differ among habitat types due to differential host quality (i.e. due to environmental rather than genetic effects). High vine vigour in commercial vineyards may provide better nutrition to the leafhoppers and hence to the developing parasitoids. The difference in grape plant species (*Vitis vinifera* in vineyards vs. *V. californica* in riparian habitats) and leafhopper species composition could also potentially affect parasitoid characteristics. We find this hypothesis less compelling as an explanation for the differences in parasitoid egg loads for several reasons. First, leafhopper egg size

Parasitoid \rightleftharpoons Parasite

6.5

TACHINID PARASITOIDS AFFECT HOST PLANT CHOICE BY CATERPILLARS TO INCREASE CATERPILLAR SURVIVAL

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Abstract. Current models of parasite–host interactions generally emphasize considerations of parasite virulence and parasite transmission rather than host responses to attack. We describe a situation in which parasitism causes a host to change its feeding behavior and this change improves the expected fitness of the host and probably the fitness of its parasites. We have found that a tachinid parasitoid (*Thelaira americana*) often emerges from its caterpillar host (*Platyrepia virginalis*) without killing the host. Whether the host caterpillar survives its parasites depends in part on what it has been eating. Unparasitized caterpillars were more likely to survive to adulthood when feeding on lupine, whereas parasitized caterpillars were more likely to survive on poison hemlock. Development time and pupal masses of caterpillars (both parasitized and unparasitized) were not found to be affected by the host plants that they fed on. Survival of fly larvae in caterpillars that we determined were parasitized using ultrasound was not affected by host plant. However, fly pupae that emerged from caterpillars that had been reared on hemlock were heavier than those emerging from lupine-fed caterpillars. This was due primarily to the direct effect of diet on the flies and less so to the indirect benefit to flies whose host caterpillars survived their parasites by feeding on hemlock.

Parasitized caterpillars were more likely to select hemlock, and unparasitized caterpillars were more likely to select lupine when offered both host plants in field tests. These results were consistent for the two years that the choice experiments were conducted. These results were also consistent with the hypothesis that caterpillars change their food plant choices so as to increase their conditional success.

Conditional food choices that increase success depending upon parasite load are well accepted for humans, controversial for other primates, and unknown for insects. If caterpillars alter their host plant choices as a result of their parasite load, then this phenomenon could help to explain the evolution of host plant choices that have defied explanation in the past. Such a suggestion assumes that nonlethal parasitism is a common phenomenon. We believe that this may be the case since we did not detect the nonlethal nature of this interaction until we began the unconventional practice of rearing in the field. Other workers have described nonlethal parasitism for several tachinid–host systems, and many families of flies are similar to tachinids except that their hosts are vertebrates; these interactions are nonlethal. Future empirical work, as well as models of parasite–host interactions, should consider the possibility that hosts alter their plant choices depending upon their parasite loads.

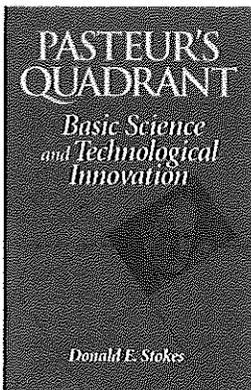
Key words: behavior; host plant choice; nonlethal parasitism; parasite-induced altered behavior; parasitoid; preference vs. performance; Tachinidae; tritrophic interactions.

INTRODUCTION

Recent models of parasite–host interactions include considerations of parasite virulence and parasite transmission (see reviews by Levin and Edén 1990, May 1991, Ebert and Hamilton 1996). These models often assume a trade-off between virulence and other fitness components for the parasite (usually transmission). For example, a highly virulent parasite may kill its host before the parasite has had a chance to reproduce or move to a new, susceptible host. Because of the linkage

between virulence and transmission, the specific biology of the host–parasite relationship determines the optimal level of virulence. However, there has been relatively little consideration of the possibility that hosts may respond to attack and that these host responses may play a role in affecting the outcome of the interaction over evolutionary time (Ebert and Hamilton 1996) or behaviorally, over shorter periods of time (Hart 1994).

We describe a situation in which a caterpillar host changes its preferences for food plants following attack by parasitoids. This parasite-induced behavioral response has profound consequences for the outcome of the parasite–host interaction. We suggest that parasite-



Working in Pasteur's Quadrant

Considerations of use?

No

Yes

		No	Yes
Yes	Bohr		Pasteur
No			Edison

Quest for fundamental understanding?

Advice from Davis Colleagues

6.7

I've seen too many colleagues fall down the math hole

Don Strong

Don't write a paper on a taxon you know nothing about

Tim Caro

Informational Ecology

6.8

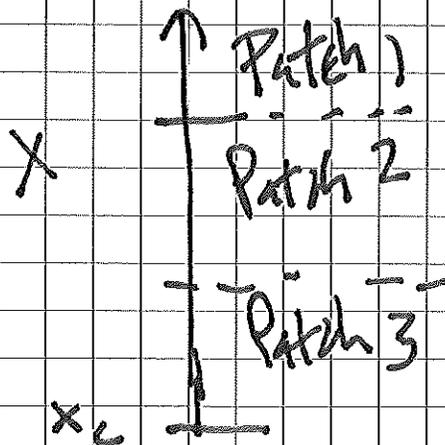
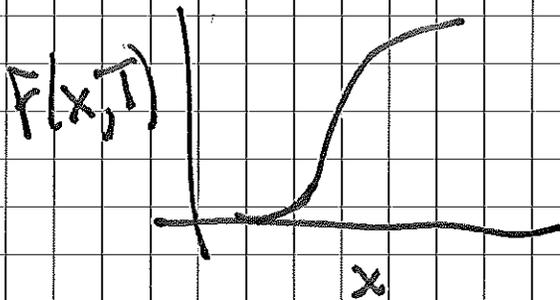
Another example: Clark and Mangel pg 239 ff

$$F(x, t) = \max_i e^{-m_i} \left[\lambda_i F(x - \alpha_i + Y_i, t+1) + (1 - \lambda_i) F(x - \alpha_i, t+1) \right]$$

Basic Parameters

Patch	λ_i	m_i
1	0	0
2	0.4	.004
3	0.6	.020

Patch 3 is both more productive ($\lambda_3 > \lambda_2$) and riskier ($m_3 > m_2$) than patch 2



How do we characterize uncertainty in m_3 ?

6.9

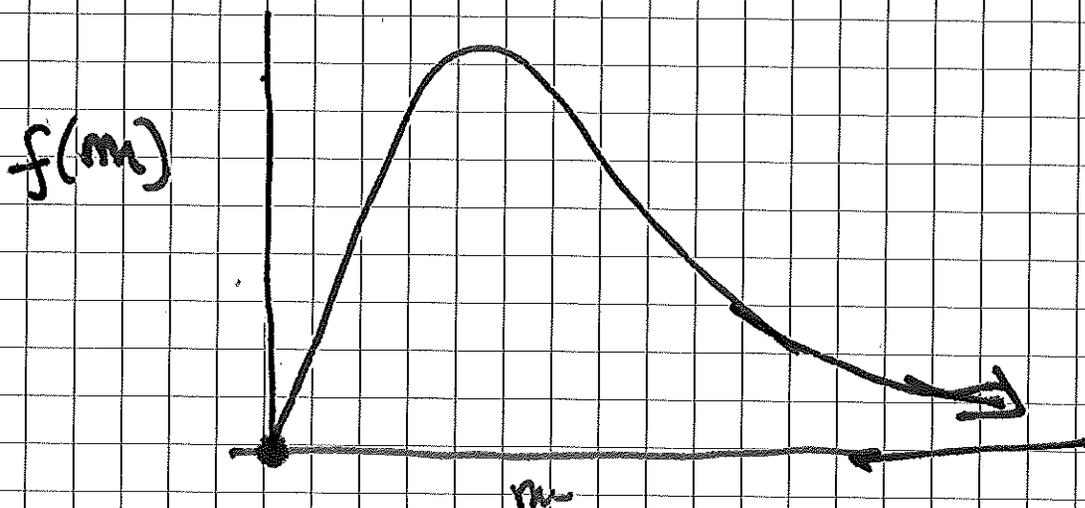
$M_3 \sim$ unknown (random) rate of mortality in patch 3

↑
continuous random variable

Probability Density Function

$$f(m) dm + o(dm)$$

$$= \Pr\{m \leq M_3 \leq m + \Delta m\}$$



We pick

$$f(m) = \frac{e^{-\alpha \cdot m} m^{\gamma-1}}{\Gamma(\gamma) \alpha^{\gamma}}$$

gamma
density

$\alpha, \gamma \sim$ parameters

$\Gamma(\gamma) \sim$ gamma function with value γ

$$\int_0^{\infty} f(m) dm = 1$$

Normalization
condition

M_3 must take some value

Suppose we have $M_3 = m_i$ w.p. p_i

$$\sum p_i = 1$$

$$\sum_i p_i \{M_3 = m_i\} = 1$$

6.11

$$\int_0^{\infty} f(m) dm = 1$$

$$\int_0^{\infty} \frac{e^{-\alpha m} m^{\nu-1}}{\Gamma(\nu)} dm = 1$$

$$\frac{\alpha^{\nu}}{\Gamma(\nu)} \int_0^{\infty} e^{-\alpha m} m^{\nu-1} dm = 1$$

$$\frac{1}{\alpha^{\nu}} \Gamma(\nu) = \int_0^{\infty} e^{-\alpha m} m^{\nu-1} dm$$

$$g(x) = \frac{1}{\sqrt{2\pi}} e^{-x^2/2} \quad \text{Normal Density}$$

$$\int_{-\infty}^{\infty} e^{-x^2/2} dx = \sqrt{2\pi}$$

$$f(m) = \frac{\alpha^\nu e^{-\alpha m} m^{\nu-1}}{\Gamma(\nu)}$$

6.12

Trust me (deh Evol Det. (ToolBox))

$$E\{M_3\} = \int_0^{\infty} m f(m) dm$$

$$= \int_0^{\infty} \frac{\alpha^\nu m e^{-\alpha m} m^{\nu-1}}{\Gamma(\nu)} dm$$

$$= \frac{\alpha^\nu}{\Gamma(\nu)} \int_0^{\infty} e^{-\alpha m} m^{\nu+1-1} dm$$

$$= \frac{\alpha^\nu}{\Gamma(\nu)} \cdot \frac{\Gamma(\nu+1)}{\alpha^{\nu+1}} = \frac{\nu}{\alpha} = E\{M_3\}$$

$$CV\{M_3\} = \frac{1}{\sqrt{\nu}}$$

~~Return to this on Weds!~~

$$\frac{\Gamma(\nu+1)}{\Gamma(\nu)} = \nu$$

$$\Gamma(\nu+1) = \nu \Gamma(\nu)$$

Bayesian Updating

$$f(m) \propto \alpha^y e^{-\alpha m} m^{y-1} \frac{1}{\Gamma(y)}$$



$$P\{M_3 \approx m\} = \frac{\alpha^y e^{-\alpha m} m^{y-1}}{\Gamma(y)}$$

We need

$P\{M_3 \approx m \mid \text{a visit to patch 3 and did not get killed}\}$

We use

$$P\{A|B\} = \frac{P\{B|A\} P\{A\}}{P\{B\}}$$

(Bayes Theorem)

$$P_A \{ M_3 \approx m \mid \text{not killed} \}$$

$$= \frac{P_B \{ \text{not killed} \mid M_3 \approx m \} P_A \{ M_3 \approx m \}}{P_B \{ \text{not killed} \}}$$

$$= \frac{e^{-\mu} \int_0^{\infty} \frac{e^{-\alpha m} m^{\nu-1}}{\Gamma(\nu)} dm}{e^{-\mu} \int_0^{\infty} \frac{e^{-\alpha m} m^{\nu-1}}{\Gamma(\nu)} dm}$$