

MODIFYING YOUR CODELoop over Time, t Looping over STATE, X

$$X_{MAX} = 0$$

Loop over I

$$X_P = X - \text{ALPHA} \cdot F + Y[I][t]$$

$$X_L = \text{Floor}[X_P]$$

$$X_U = X_L + 1 \quad (\text{check that } X_U \leq X_{MAX})$$

$$Q_X = X_U - X_P$$

$$V[I][X][t]$$

$$= (Q_X * F[X_L][t+1]$$

$$+ (1 - Q_X) * F[X_U][t+1])$$

~~for~~

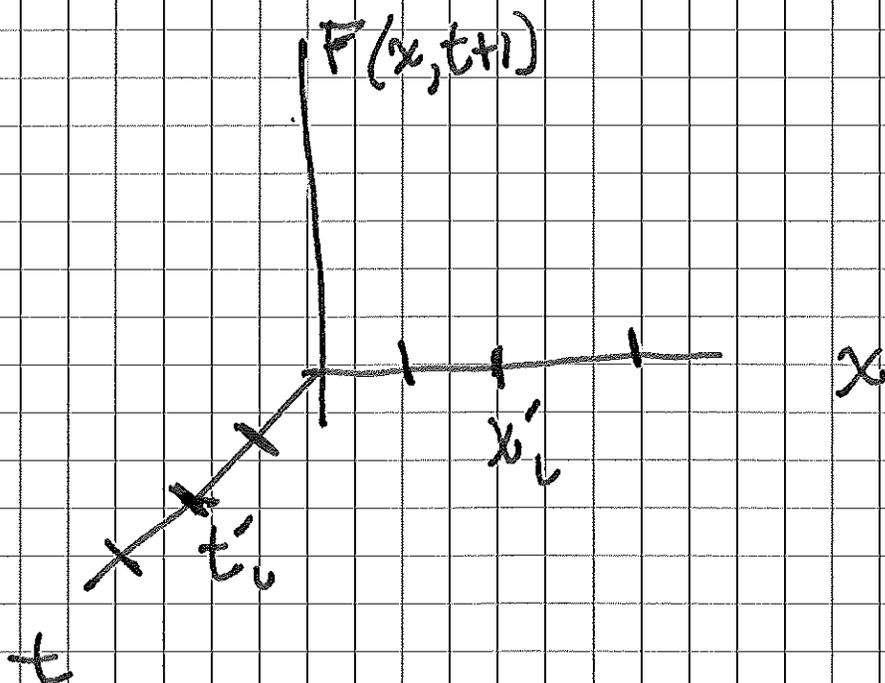
$$(1 - \text{BETA}[I]) \text{LAMBDA}[I]$$

$$+ (1 - \text{BETA}[I]) (1 - \text{LAMBDA}[I]) F[X_P][t+1]$$

10/2

FOR OUR AWESOME EQN (PG 10.8) WE COULD HAVE

$x'_i, t'_i(h) \sim$ both non integers



Canonical Equation for Activity Choice
(CEAC)

Alternative: Accumulate Fitness Potentially
At Every Period Between
 t and T

10.13

David Lach (Melissa)

15 April 2013

An Algorithm for Discovery

As academic physicians, we are experiencing the rush to restructure medical services and have participated in the development of algorithms for the evaluation and treatment of patients. It has been argued that such algorithms are a critical tool for evidence-based medicine, for improving patient management, and for raising the community standard of clinical care.

One day, during a particularly lengthy commute in our carpool, we began to wonder whether the process of creating new knowledge—asking the right question, pursuing the unknown, making discoveries—might also benefit from such an algorithmic approach. Surely a formula for boosting the rate and magnitude of discoveries would be most welcome. Of course, there are many great treatises on discovery in science, but we were thinking of something more compact for everyday use, a kind of flow chart that could be carried on a laminated card. Many carpools later, we came up with the solution shown on the right.

After rigorous computer simulations of this algorithm's performance over a broad range of parameters, we unexpectedly discovered that its properties could be reduced to five simple principles.

1. Slow down to explore. Discovery is facilitated by an unhurried attitude. We favor a relaxed yet attentive and prepared state of mind that is free of the checklists, deadlines, and other exigencies of the workday schedule. Resist the temptation to settle for quick closure and instead actively search for deviations, inconsistencies, and peculiarities that don't quite fit. Often hidden among these anomalies are the clues that might challenge prevailing thinking and conventional explanations.

2. Read, but not too much. It is important to master what others have already written. Published works are the forum for scientific discourse and embody the accumulated experience of the research community. But the influence of experts can be powerful and might quash a nascent idea before it can take root. Fledgling ideas need nurturing until their viability can be tested without bias. So think again before abandoning an investigation merely because someone else says it can't be done or is unimportant.

3. Pursue quality for its own sake. Time spent refining methods and design is almost always rewarded. Rigorous attention to such details helps to avert the premature rejection or acceptance of hypotheses. Sometimes, in the process of perfecting one's approach, unexpected discoveries can be made. An example of this is the background radiation attributed to the Big Bang, which was identified by Penzias and Wilson while they were pursuing the source of a noisy signal from a radio telescope. Meticulous testing is a key to generating the kind of reliable information that can lead to new breakthroughs.

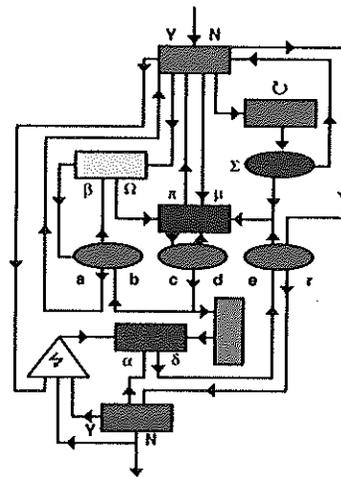
4. Look at the raw data. There is no substitute for viewing the data at first hand. Take a seat at the bedside and interview the patient yourself; watch the oscilloscope trace; inspect the gel while still wet. Of course, there is no question that further processing of data is essential for their management, analysis, and presentation. The problem is that most of us don't really understand how automated packaging tools work. Looking at the raw data provides a check against the automated averaging of unusual, subtle, or contradictory phenomena.

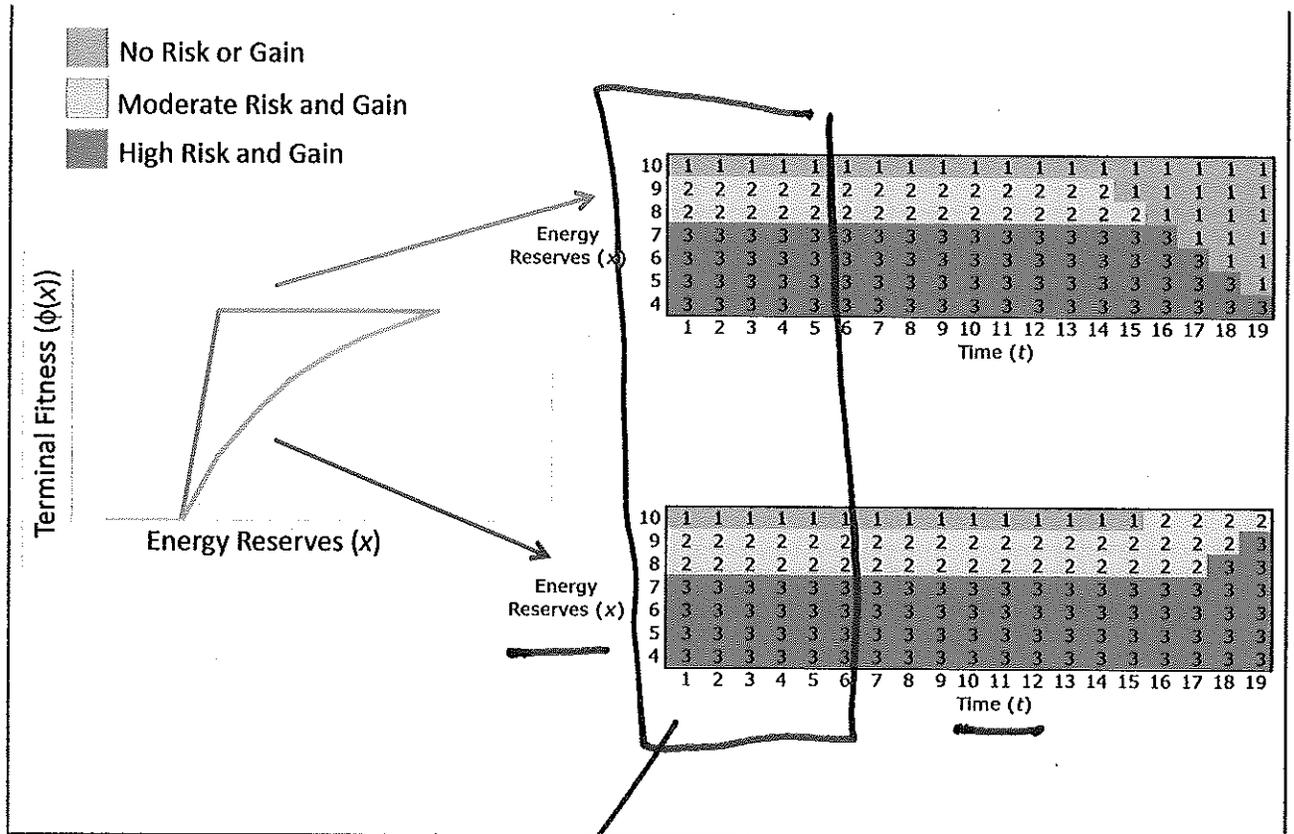
5. Cultivate smart friends. Sharing with a buddy can sharpen critical thinking and spark new insights. Finding the right colleague is in itself a process of discovery and requires some luck. Sheer intelligence is not enough; seek a pal whose attributes are also complementary to your own, and you may be rewarded with a new perspective on your work. Being this kind of friend to another is the secret to winning this kind of friendship in return.

Although most of us already know these five precepts in one form or another, we have noticed some difficulty in putting them into practice. Many obligations appear to erode time for discovery. We hope that this essay can serve as an inspiration for reclaiming the process of discovery and making it a part of the daily routine. In 1936, in *Physics and Reality*, Einstein wrote, "The whole of science is nothing more than a refinement of everyday thinking." Practicing this art does not require elaborate instrumentation, generous funding, or prolonged sabbaticals. What it does require is a commitment to exercising one's creative spirit—for curiosity's sake.

David Paydarfar and William J. Schwartz

David Paydarfar and William J. Schwartz are in the Department of Neurology, University of Massachusetts Medical School, 55 Lake Avenue North, Worcester, MA 01655. This paper was adapted from lectures given at the University of North Carolina, Chapel Hill, and the University of California, San Francisco, Schools of Medicine.





$x = 6.2$

$x = 7.2$

stochastic decisions

Aus 216 SDE

15.1

"We don't truncate, 'cause we interpolate"

What about non-integer states in forward iteration.

If $X_k(t) \sim$ not an integer

① If the decision for $\text{int}[X_k(t)]$
and $\text{int}[X_k(t)]+1$ is the same
 \Rightarrow nothing to think about

② Otherwise, you need to make a decision.

A) Pick a coin of the two

B) Compare fitness of the two choices and
do that giving the higher fitness

C) Randomly choose between the two

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

Anthropogenic mortality

Visiting multiple patches before returning home

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)

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

Patch depletion

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

Dependent young

Learning

Schooling behavior

Spatial structure and networks of patches

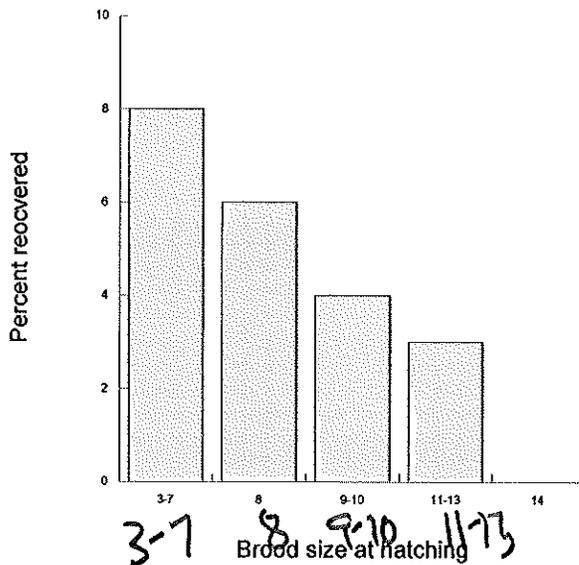
Games against conspecifics

Predator-prey games

15.3

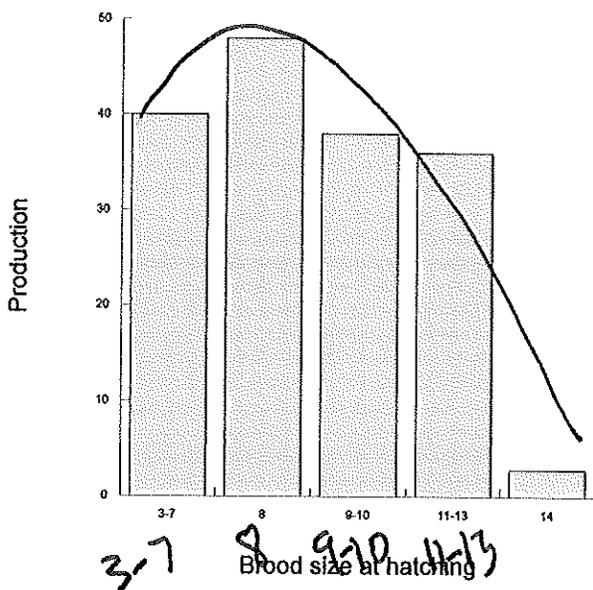


Whytham Wood



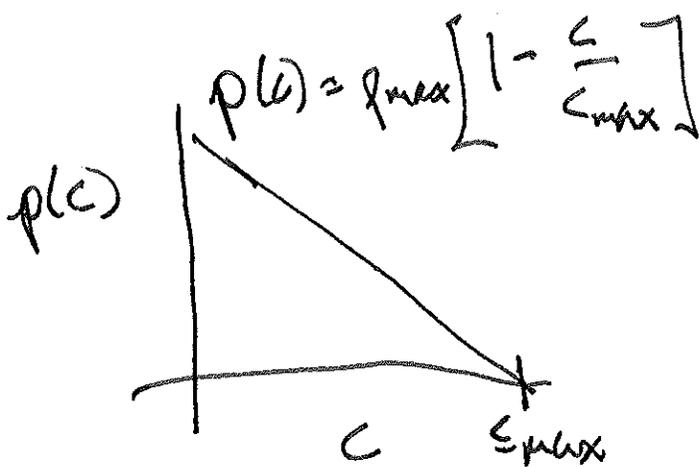
offspring per parent
individual survival

3-7 8 9-10 11-13
Brood size at hatching

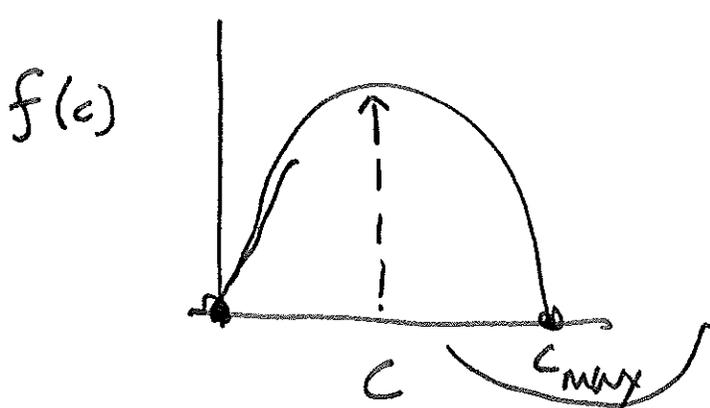


Mom's perspective

goes into the next generation



$f(c) = \text{fitness to mom from the clutch} = c \cdot p(c)$



$= c p_{max} \left[1 - \frac{c}{c_{max}} \right]$

LACK
Lack clutch size
(LCS)



Aphytis linguensis

Jay Rosen UCD

$$\underline{S(c)} = 0.245 - 0.0223(c - 1) \quad \underline{\text{size}}$$

$$E(S) = \max\{181.8S(c) - 26.7, 0\} \quad \text{eggs}$$

$$f(c) = cE(S(c)) \quad \leftarrow \# \text{ of stand offspring} //$$

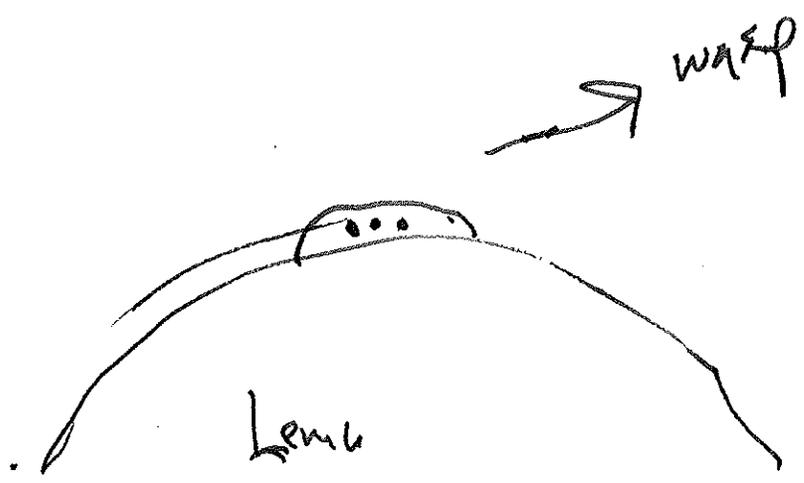
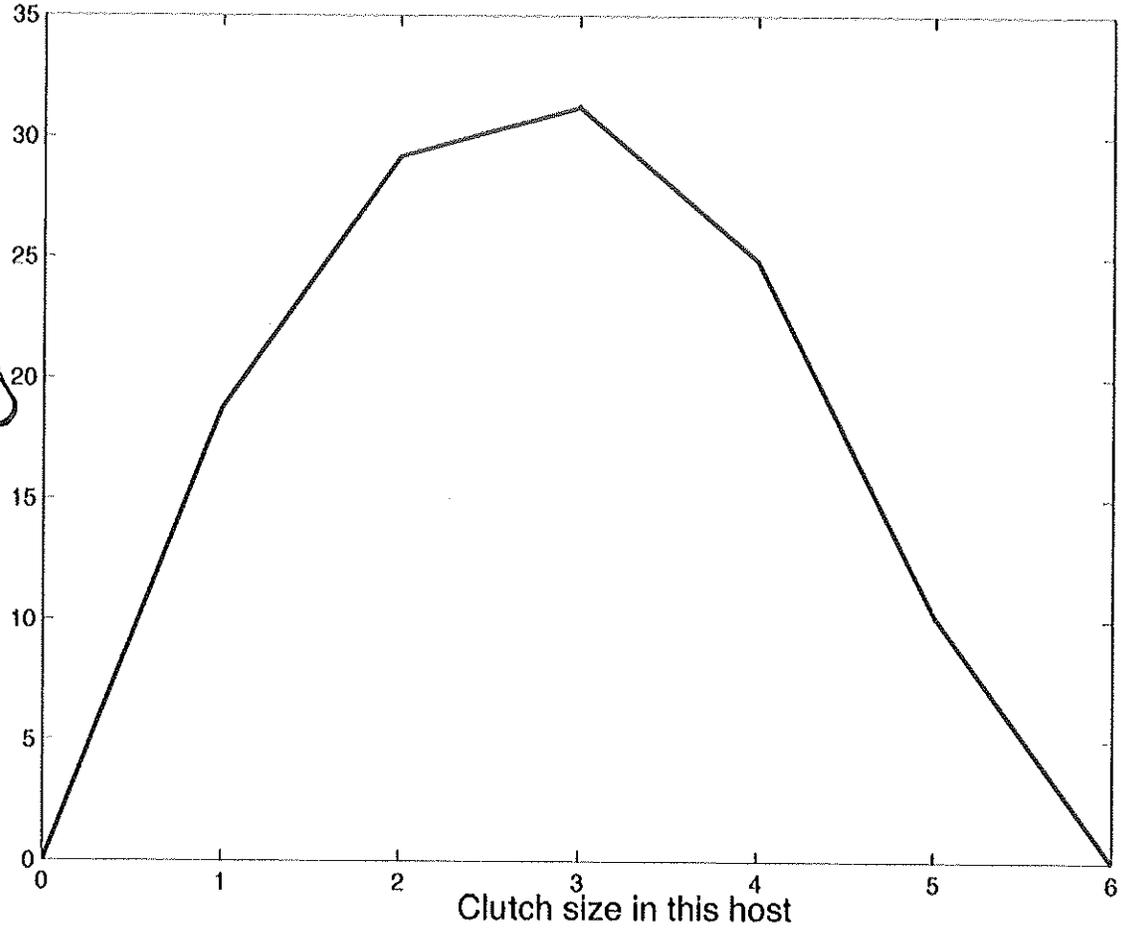
$S(c) \sim$ egg spring size

$E(S) \sim$ egg spring eggs

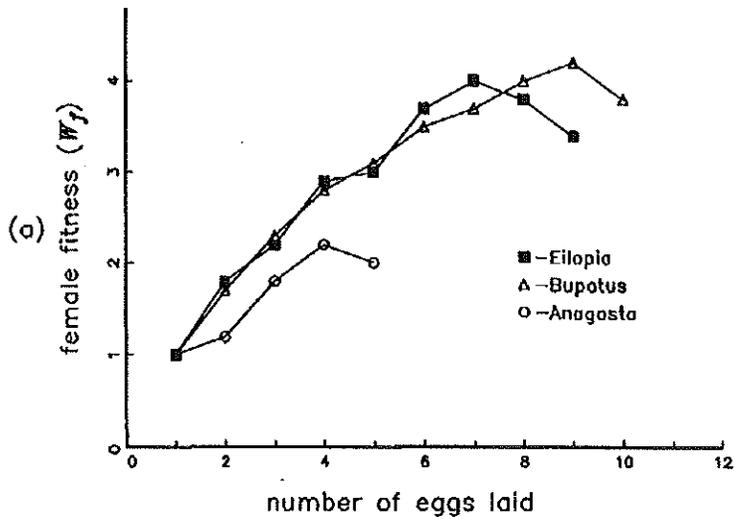
Insect parasitoids

15.6

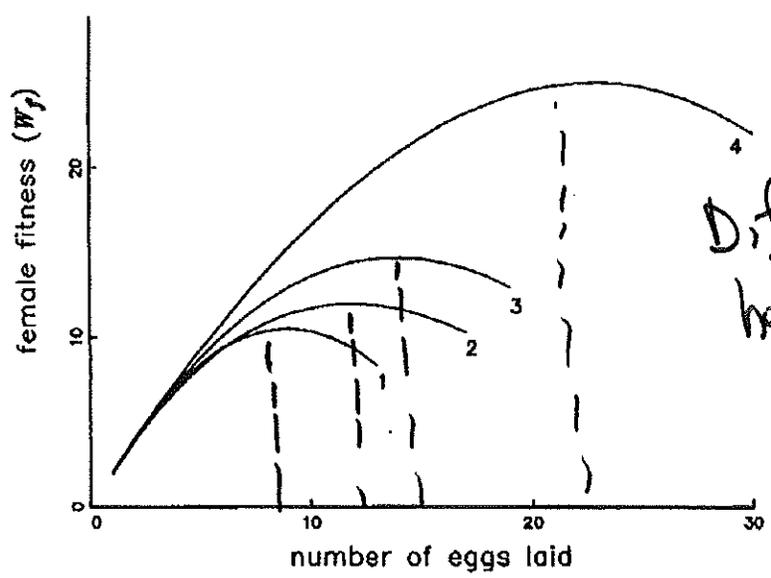
Grand-offspring



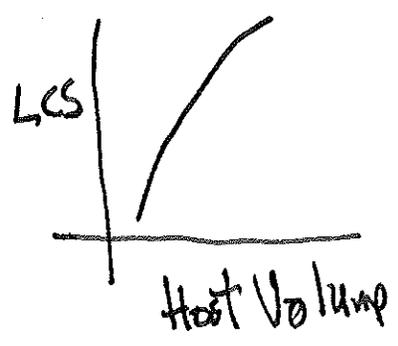
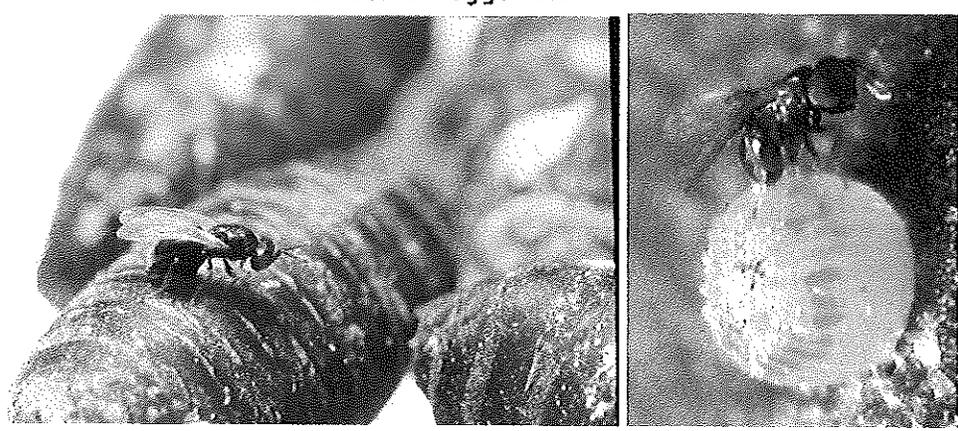
15.7

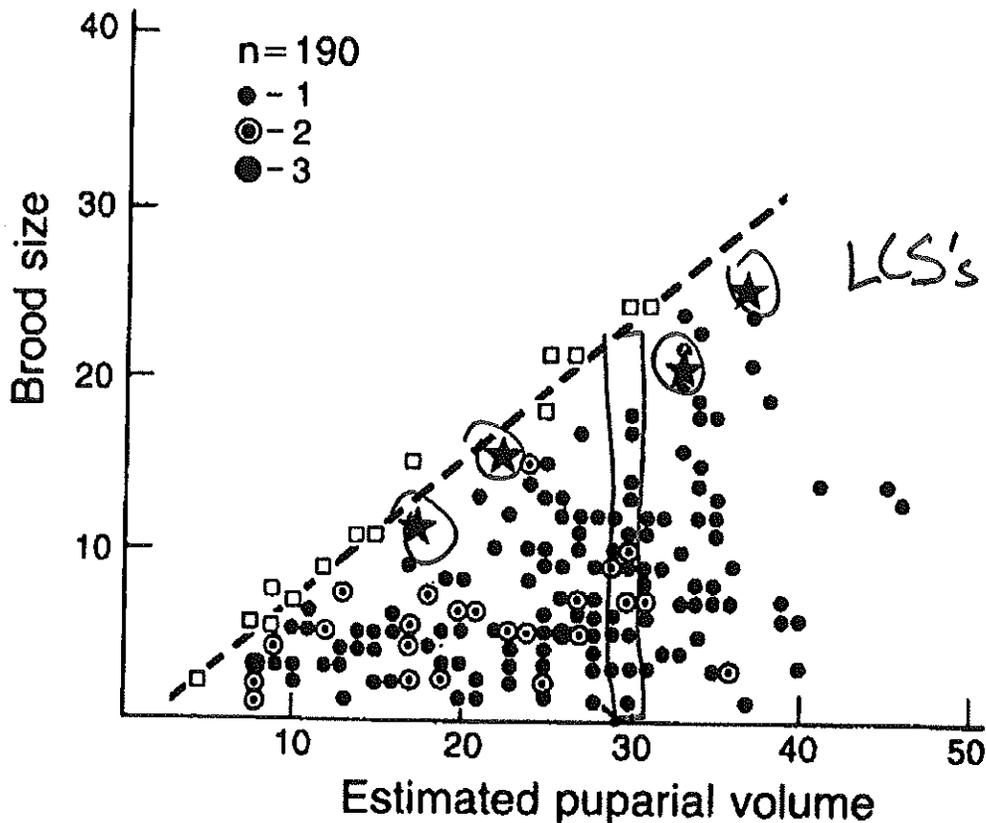


E Connor
 S Skinner
 1984
 Florida
 Entomologist
 14: 383



Different
 host volumes





E Charnov and S Skinner. 1984. Florida Entomologist 14:383

- 1) Almost all clutches smaller than Least Clutch Size
- 2) Small clutches more likely

Ch4, MLC

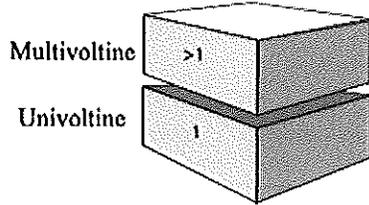
Ch4, CAM

Ch4, ToolBox

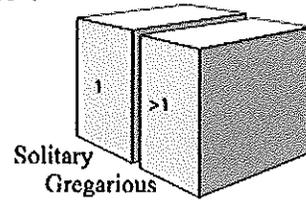
Insect Life Histories

15.9

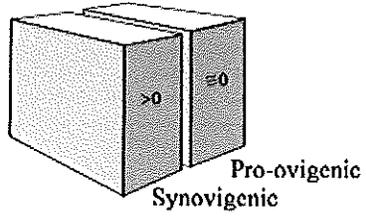
a) Generations per Year:



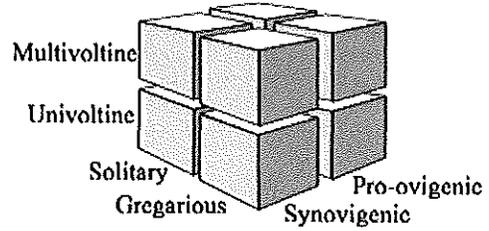
b) Eggs per Host:



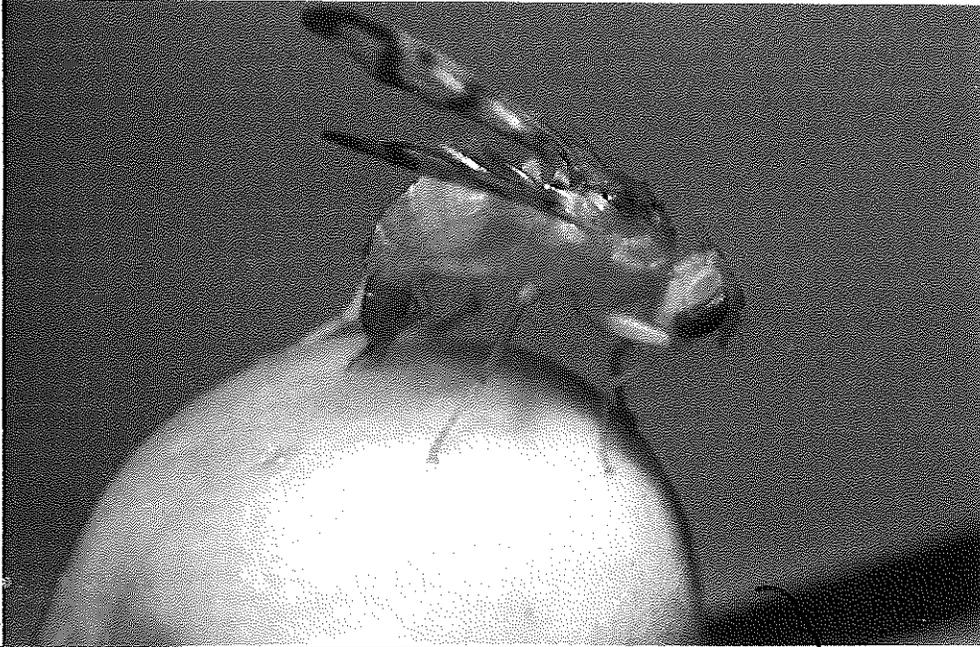
c) Egg Production After Emergence:



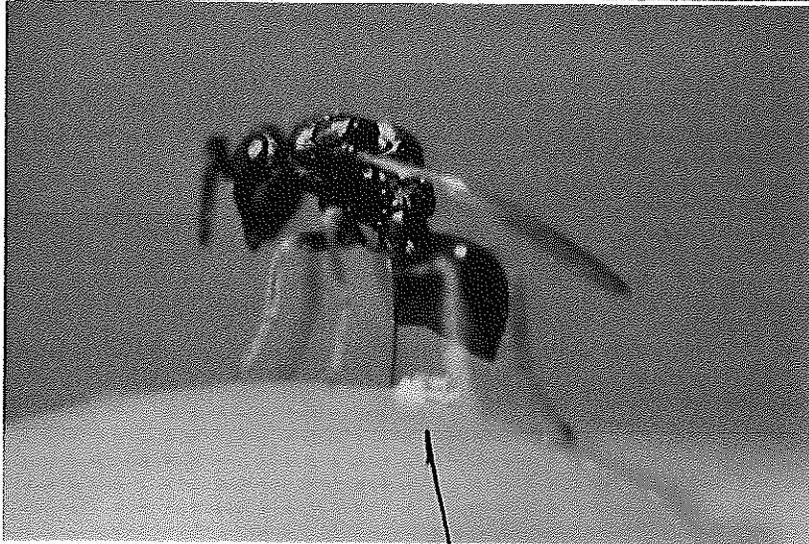
d) Combining the characteristics:



15.10



Rhagoletis
basiola
(Rose hip
fly)

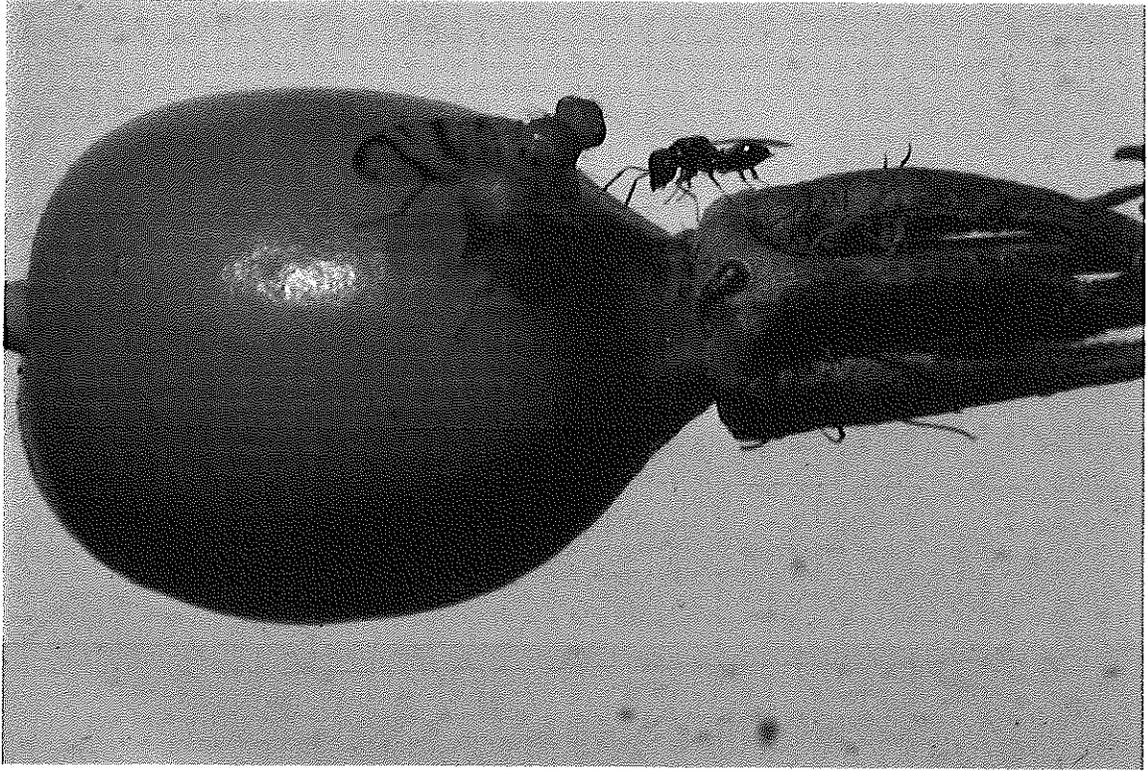


Halticoptera rosae

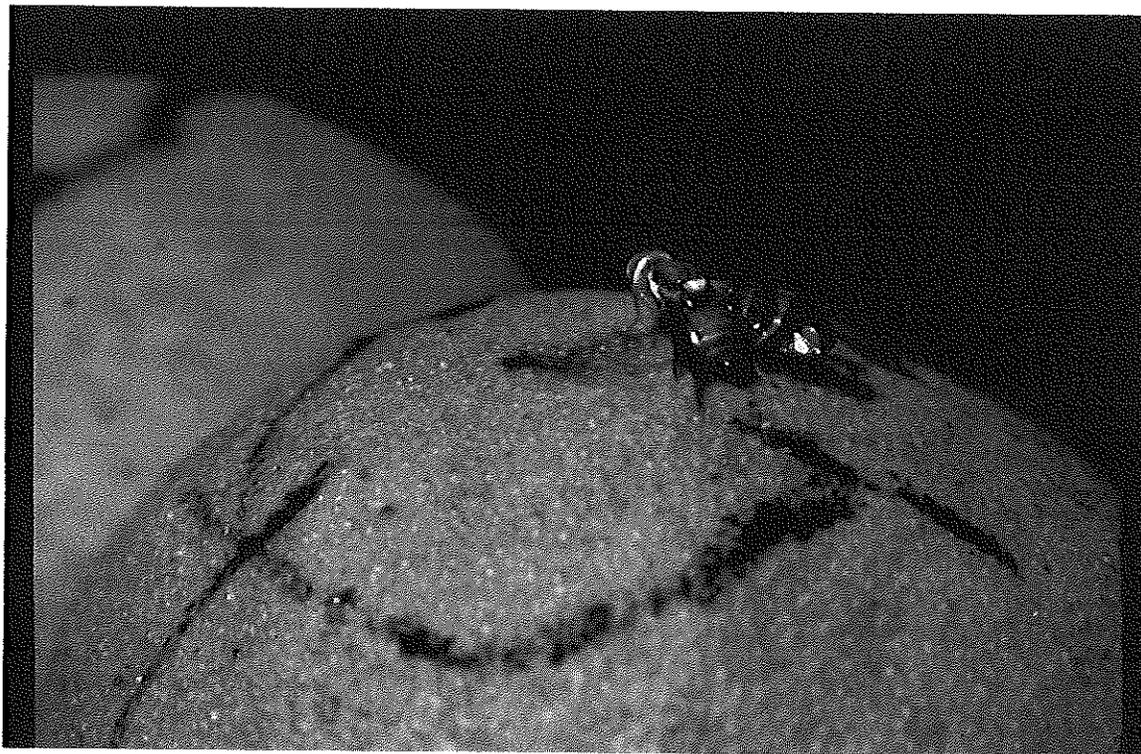
SD Rothberg
SFU

super-parasitism

15.11

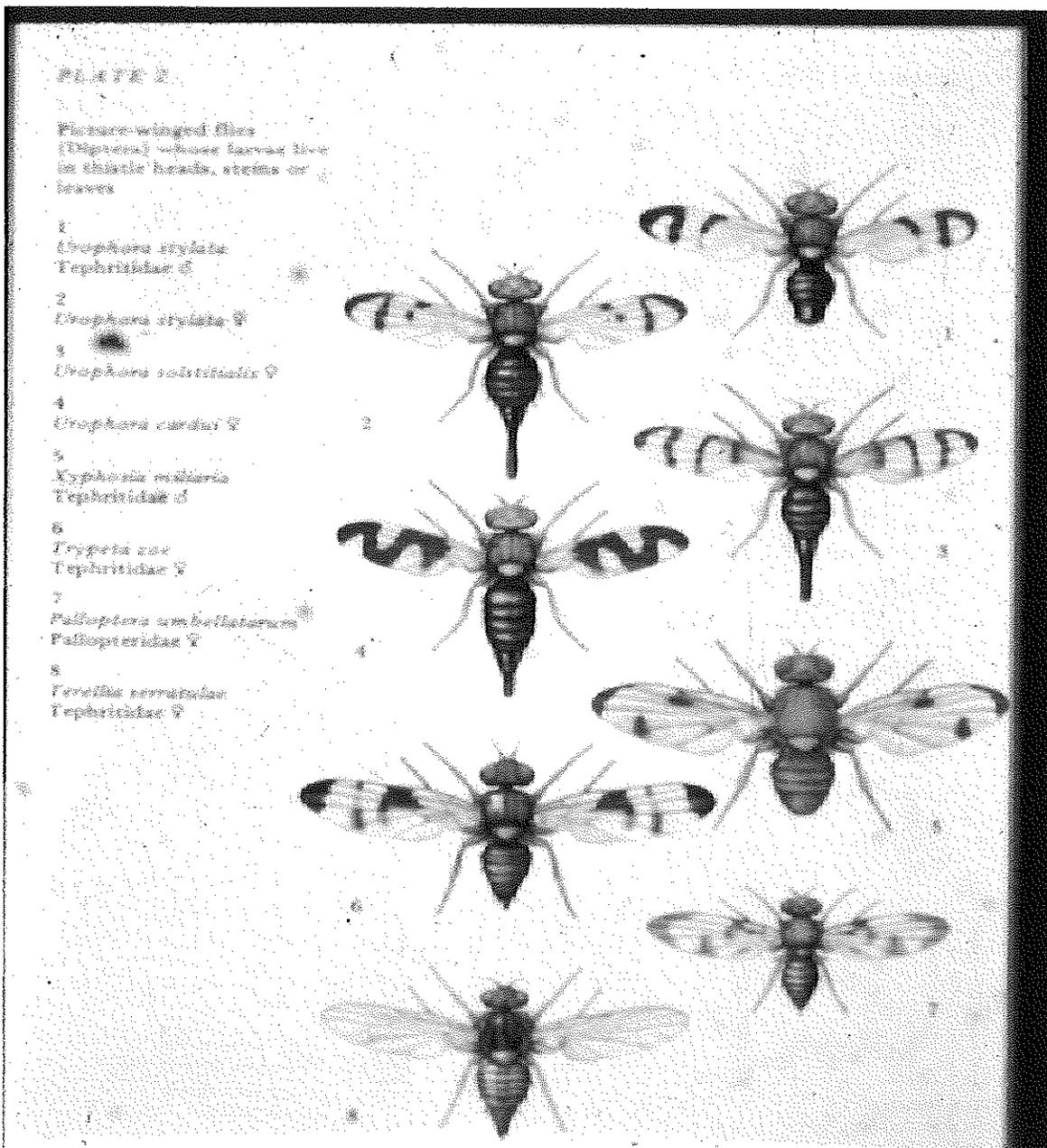


15.12



R.
completa



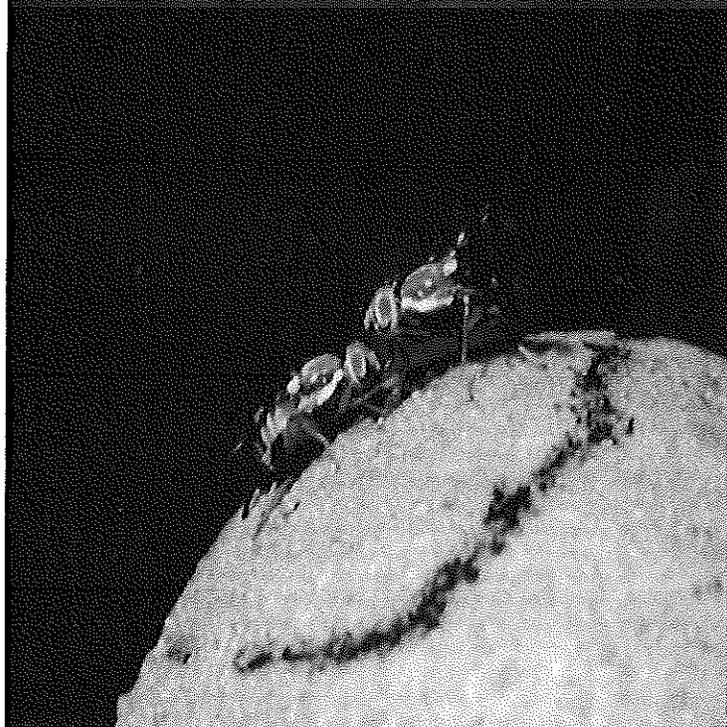
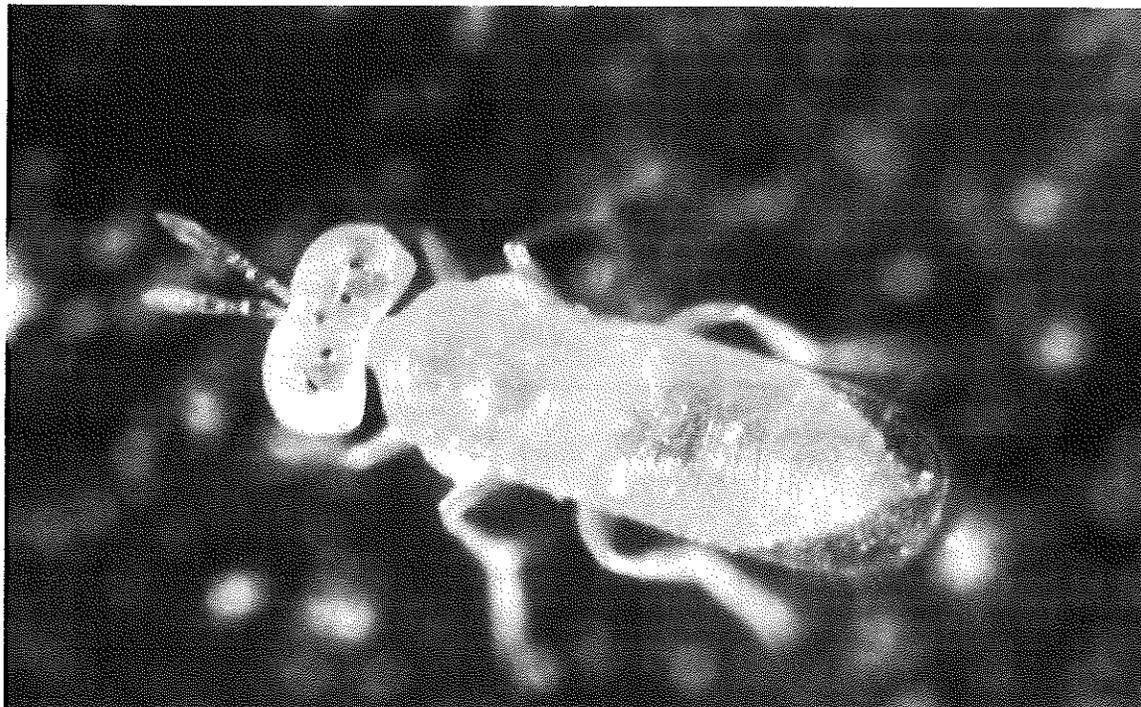


True fruit flies

15.16

→

15.18



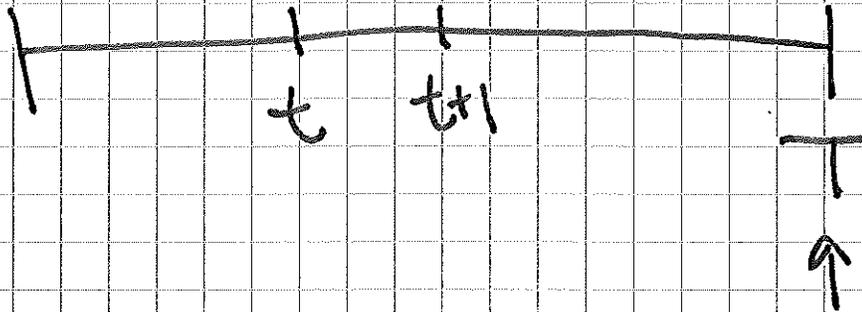
15.19



Leptopilina.

Univoltine, Solitary, Proovigenic Parasitoid

5.20



Physiology

$X(t) = \#$ of eggs remaining at time t

fixed and known in evolutionary time

$\tau =$ time spent ovipositing. (variable handling time problem)

~~$X(t)$~~ \rightarrow ~~$X(t)$~~

If $X(t) = x$

$\rightarrow X(t+\tau) = x$ no oviposition

$\rightarrow X(t+\tau) = x-1$ if oviposition

The Environment

15.01²

Two kinds of hosts

in one period of search

	Prob of Encounter	Increment in fitness from an oviposition
Unparasitized	p_u	f_u
Previously parasitized	p_p	f_p

$$0 < p_u, p_p$$

$$p_u + p_p \leq 1$$

$$0 < f_u, f_p$$

$$f_u > f_p$$

Mortality Rates

$$m_s < m_o$$

$m_s \sim$ per period rate of mortality when she is searching

$m_o \sim$ per period rate of mortality when she is ovipositing

Hempel and Mangel ~ 1999, 2000

lifetime Fitness Function

$$F(x, t) = \max E \left\{ \text{accumulated fitness from} \right. \\ \left. \text{ov position between } t \text{ and} \right. \\ \left. T \mid X(t) = x \right\}$$

$$F(x, T) = 0 \quad \text{end condition}$$

$$F(x, t) = (1 - p_u - p_p) e^{-m_s \cdot 1} F(x, t+1) \\ + p_u \left[f_u + e^{-(m_s + m_d \cdot \tau)} F(x-1, t+\tau) \right] \\ + p_p \max \left[e^{-m_s} F(x, t+1); \right. \\ \left. f_p + e^{-(m_s + m_d \cdot \tau)} F(x-1, t+\tau+1) \right]$$

\leftarrow reject
 \leftarrow accept

$$\max [A; B] = \begin{cases} A & \text{if } A \geq B \\ B & \text{if } A < B \end{cases}$$

17 April

Plan

No class 24 April (Working Day)

One Day in May 13, 15, 22 May

Presenting Your Project

2 Days for coding

Papers We Like

- The paper you like goes into the Dropbox folder
- 2 pages about why you like it directly to me

Why you like it
How might you use it

by email

One of historical Wednesday



Purcell and Brodin 2007.pdf

Factors influencing route choice by avian migrants: A dynamic programming model of Pacific brant migration

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Available online 4 September 2007

Abstract

We used stochastic dynamic programming to investigate a spectacular migration strategy in the black brant *Branta bernicla nigricans*, a species of goose. Black brant migration is well suited for theoretical analysis since there are a number of existing strategies that easily can be compared. In early autumn, almost the entire population of the black brant gathers at Izembek Lagoon on the Alaska Peninsula to stage and refuel before the southward migration. There are at least three distinct strategies, with most geese making a spectacular direct migration more than 5000 km across the Gulf of Alaska to their wintering grounds in southern Baja California or mainland Mexico. This is a potentially dangerous strategy since foraging is not possible during the overseas passage. Some individuals instead use shorter flights to make a detour along the coast, a longer route that all individuals use for northwards migration in spring. Since flight costs accelerate with increasing body mass, migration by short flights is energetically cheaper than long-distance flights. A small but increasing part of the population has recently begun to winter at Izembek. We investigated this migration under two different suppositions using a dynamic state variable model. First, if the geese are free to make a strategic choice, under what assumptions should they prefer direct migration and under what assumptions should they prefer detour migration/winter residency? Second, provided that the dominating direct migration strategy is optimal, what conditions will force the geese to go for detour migration/winter residency? In the second case the geese may try to follow an optimal direct migration strategy, but stochastic events may force them to choose a suboptimal policy. We also simulated possible effects of global warming. The model suggests that the fuel level at arrival in Izembek and fuel gain rates are key factors and that tail winds must have been reliable in the past, otherwise direct migration could not have evolved. It also suggests that a change to milder winters may promote an unexpectedly abrupt change from long-distance to short-distance migration or winter residency. Finally, it produced a number of predictions that might be testable in the field.

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Keywords: Avian migration; *Branta bernicla nigricans*; Dynamic programming; Brant; Migration strategy

1. Introduction

1.1. Bird migration

Bird migration is a complex behaviour where the optimal strategy depends on many interacting factors, both internal and external. In most cases migration is risky and energetically demanding, making it likely that selection

for optimal strategies is strong. Stochastic dynamic programming is especially well suited to model behaviour for which theoretical analysis requires inclusion of many factors to become meaningful. With this technique many factors can be included after which they can be manipulated one at a time.

Migrating birds face a wide variety of environmental conditions and scenarios that may affect decisions about when, where, and how to migrate. For example, weather, bird condition, and geography are important (Alerstam et al., 2003). The effect of wind is a key factor that should influence the timing and energetics of migration in most bird species (Richardson, 1978; Hedenström et al., 2002; Green and Piersma, 2003).

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McDonald-Madden et al. 2010.pdf

Active adaptive conservation of threatened species in the face of uncertainty

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HUGH P. POSSINGHAM,^{1,2} MENNA E. JONES,^{5,6} JOSLIN L. MOORE,⁷ TRACY M. ROUT,⁷ PETER A. VESK,⁷
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Abstract. Adaptive management has a long history in the natural resource management literature, but despite this, few practitioners have developed adaptive strategies to conserve threatened species. Active adaptive management provides a framework for valuing learning by measuring the degree to which it improves long-run management outcomes. The challenge of an active adaptive approach is to find the correct balance between gaining knowledge to improve management in the future and achieving the best short-term outcome based on current knowledge. We develop and analyze a framework for active adaptive management of a threatened species. Our case study concerns a novel facial tumor disease affecting the Australian threatened species *Sarcophilus harrisi*: the Tasmanian devil. We use stochastic dynamic programming with Bayesian updating to identify the management strategy that maximizes the Tasmanian devil population growth rate, taking into account improvements to management through learning to better understand disease latency and the relative effectiveness of three competing management options. Exactly which management action we choose each year is driven by the credibility of competing hypotheses about disease latency and by the population growth rate predicted by each hypothesis under the competing management actions. We discover that the optimal combination of management actions depends on the number of sites available and the time remaining to implement management. Our approach to active adaptive management provides a framework to identify the optimal amount of effort to invest in learning to achieve long-run conservation objectives.

Key words: active adaptive management; Bayesian updating; decision theory; learning; Markov decision process; *Sarcophilus harrisi*; stochastic dynamic programming; Tasmania, Australia; Tasmanian devil facial tumor disease.

INTRODUCTION

Conservation management faces the challenge of making good decisions despite uncertainty about both the ecology of the system to be managed and impact of the management options on that system (Burgman et al. 2005). Uncertainty can manifest itself in a number of aspects of knowledge (Regan et al. 2002). There may be uncertainty around parameter estimates which lead us to question the output of models (Caswell 2001). Managers may also be uncertain about the model they have chosen

to represent the system (Chatfield 1995, Regan et al. 2002). Because models provide valuable tools with which to investigate the response of systems to different management scenarios and are commonly used to make conservation decisions (e.g., Possingham et al. 1993, Punt and Smith 1999), a number of techniques have been proposed that quantify model uncertainty (Burnham and Anderson 2002, Wintle et al. 2003) and facilitate decisions that are coherent in the face of model uncertainty (Burgman et al. 1993, Drechsler et al. 1998, Shea and Possingham 2000, Yokomizo et al. 2003, Regan et al. 2005, 2006).

Some uncertainty is effectively irreducible (e.g., natural variation/stochasticity), while other forms of uncertainty may be reduced through learning. What is not captured within most uncertainty analyses is our ability to learn about a system while we are managing

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AFRICAN STUDIES CENTER - UNIVERSITY OF PENNSYLVANIA

17.3

"Letter from a Birmingham Jail [King, Jr.]"

16 April 1963

April 16, 1963

My Dear Fellow Clergymen:

While confined here in the Birmingham city jail, I came across your recent statement calling my present activities "unwise and untimely." Seldom do I pause to answer criticism of my work and ideas. If I sought to answer all the criticisms that cross my desk, my secretaries would have little time for anything other than such correspondence in the course of the day, and I would have no time for constructive work. But since I feel that you are men of genuine good will and that your criticisms are sincerely set forth, I want to try to answer your statement in what I hope will be patient and reasonable terms.

I think I should indicate why I am here in Birmingham, since you have been influenced by the view which argues against "outsiders coming in." I have the honor of serving as president of the Southern Christian Leadership Conference, an organization operating in every southern state, with headquarters in Atlanta, Georgia. We have some eighty five affiliated organizations across the South, and one of them is the Alabama Christian Movement for Human Rights. Frequently we share staff, educational and financial resources with our affiliates. Several months ago the affiliate here in Birmingham asked us to be on call to engage in a nonviolent direct action program if such were deemed necessary. We readily consented, and when the hour came we lived up to our promise. So I, along with several members of my staff, am here because I was invited here. I am here because I have organizational ties here.

But more basically, I am in Birmingham because injustice is here. Just as the prophets of the eighth century B.C. left their villages and carried their "thus saith the Lord" far beyond the boundaries of their home towns, and just as the Apostle Paul left his village of Tarsus and carried the gospel of Jesus Christ to the far corners of the Greco Roman world, so am I compelled to carry the gospel of freedom beyond my own home town. Like Paul, I must constantly respond to the Macedonian call for aid.

Moreover, I am cognizant of the interrelatedness of all communities and states. I cannot sit idly by in Atlanta and not be concerned about what happens in Birmingham. Injustice anywhere is a threat to justice everywhere. We are caught in an inescapable network of mutuality, tied in a single garment of destiny. Whatever affects one directly, affects all indirectly. Never again can we afford to live with the narrow, provincial "outside agitator" idea. Anyone who lives inside the United States can never be considered an outsider anywhere within its bounds.

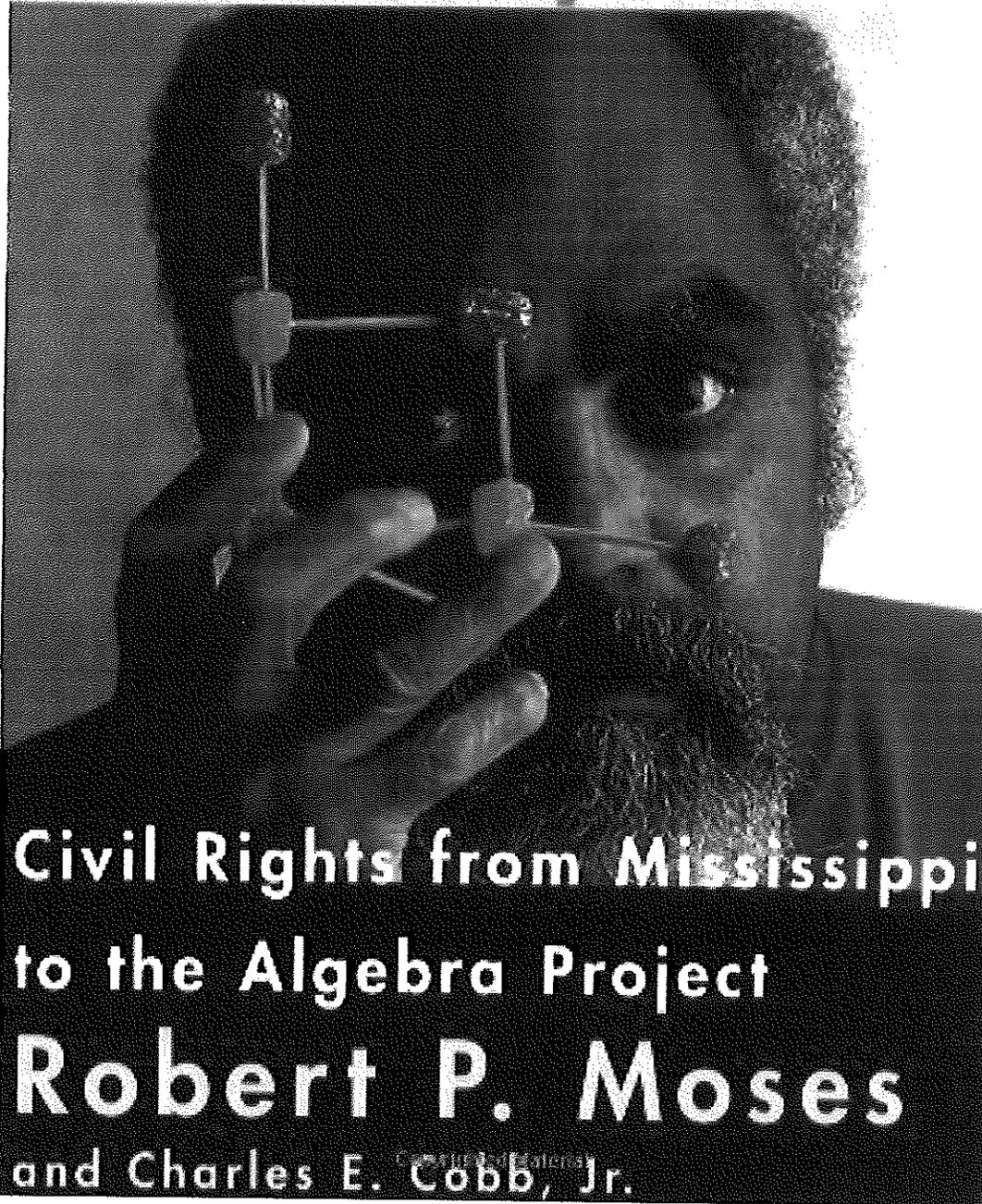
You deplore the demonstrations taking place in Birmingham. But your statement, I am sorry to say, fails to express a similar concern for the conditions that brought about the demonstrations. I am sure that none of you would want to rest content with the superficial kind of social analysis that deals merely with effects and does not grapple with underlying causes. It is unfortunate that demonstrations are taking place in Birmingham, but it is even more unfortunate that the city's white power structure left the Negro community with no alternative.

In any nonviolent campaign there are four basic steps: collection of the facts to determine whether injustices exist; negotiation; self purification; and direct action. We have gone through all these steps in Birmingham. There can be no gainsaying the fact that racial injustice engulfs this community. Birmingham is probably the most thoroughly segregated city in the United States. Its ugly record of brutality is widely known. Negroes

"Robert Moses is the towering activist/intellectual of his generation—a grassroots freedom fighter of quiet dignity and incredible determination." —Cornel West

17.4

radical equations



Civil Rights from Mississippi

to the Algebra Project

Robert P. Moses

and Charles E. Cobb, Jr.

SPT Problems in lieu of project

17.5

Review Questions Don't Need to Be Submitted

Univoltine, Pro-ovigenic, Solitary Parasitoid

$$F(x, t) = \max_x E \left\{ \text{fitness from ovipositions between } t \text{ and } T \mid X(t) = x \right\}$$

End condition

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

$$F(x, t) = (1 - p_u - p_p) e^{-m_s} F(x, t+1)$$

$$+ p_u \left[f_u + e^{-(m_s + m_o T)} F(x-1, t+1+T) \right]$$

skips/rejects

$$+ p_p \max \left[e^{-m_s} F(x, t+1); \right.$$

$$\left. f_p + e^{-(m_s + m_o T)} F(x-1, t+1+T) \right]$$

accepts / super parasitize

"oviposition is an opportunity cost"

Procedure

17.6

End Condition

loop over x , set

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

Next x

MAXIMUM EGG COMPLET
MAXIMUM egg complet

DPE

loop from $t = T-1$ to 1

loop over $x = 1$ to x_{max}

$$F(x, t) = (1 - p_u - p_p) e^{-m_s} F(x, t+1) \quad \text{NO encounter}$$

Replace $F(x, t)$ by

$$F(x, t) + p_u \left[f_u + e^{-(m_s + m_b t)} F(x-1, t') \right]$$

$$\text{where } t' = \min[t+1, T]$$

$$V_{rej} = e^{-m_s} F(x, t+1)$$

$$V_{sup} = f_p + e^{-(m_s + m_b t)} F(x-1, t')$$

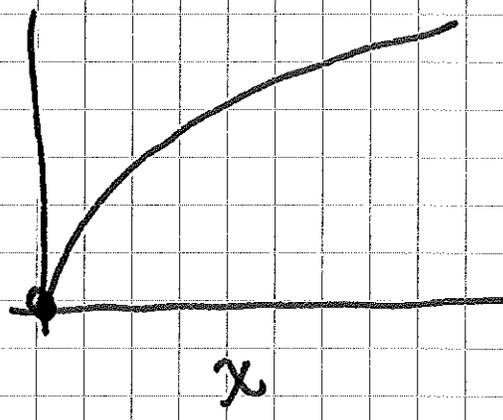
Replace $F(x, t)$ by

$$F(x, t) + p_p \max[V_{rej}, V_{sup}]$$

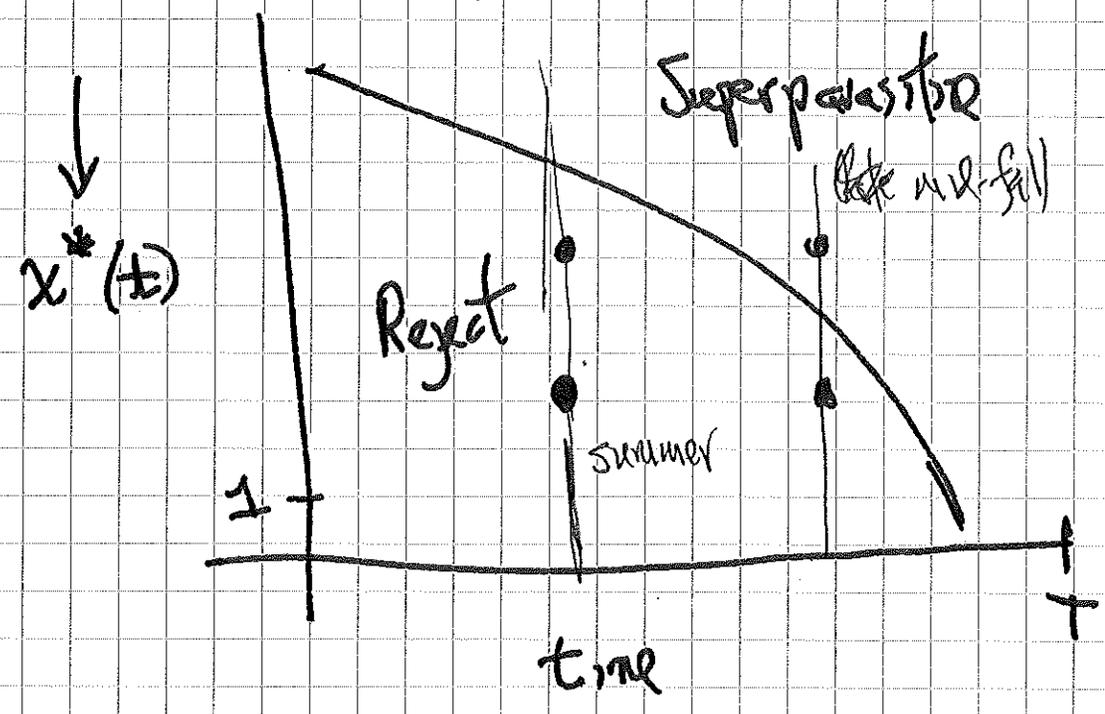
When we hit Killar Time [L.P. code is done]
we have

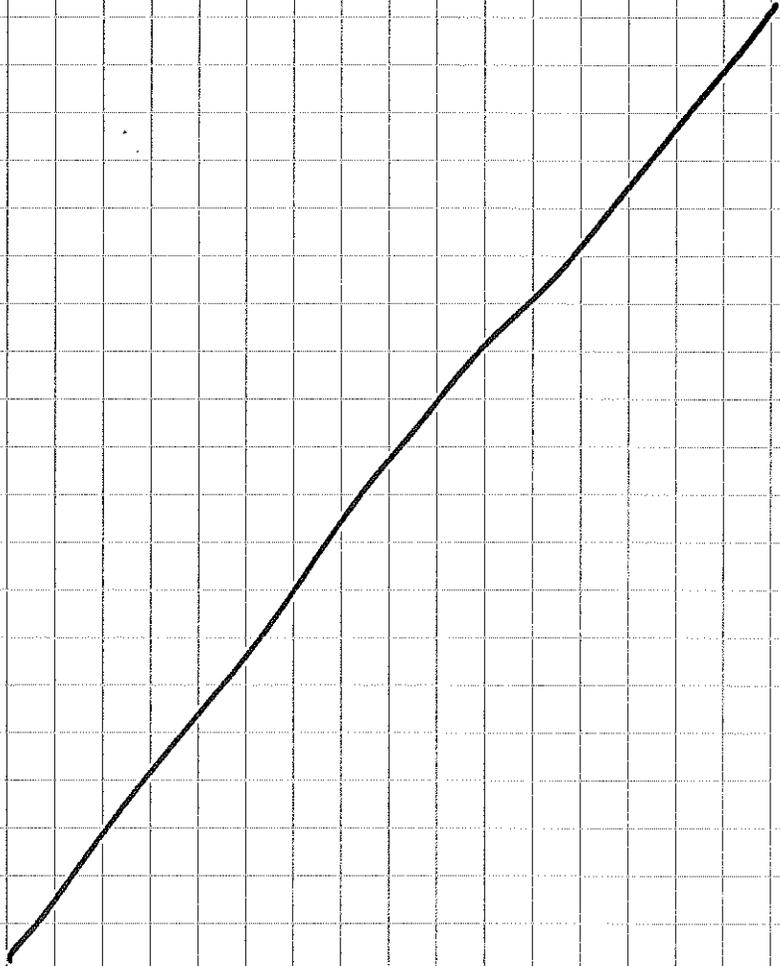
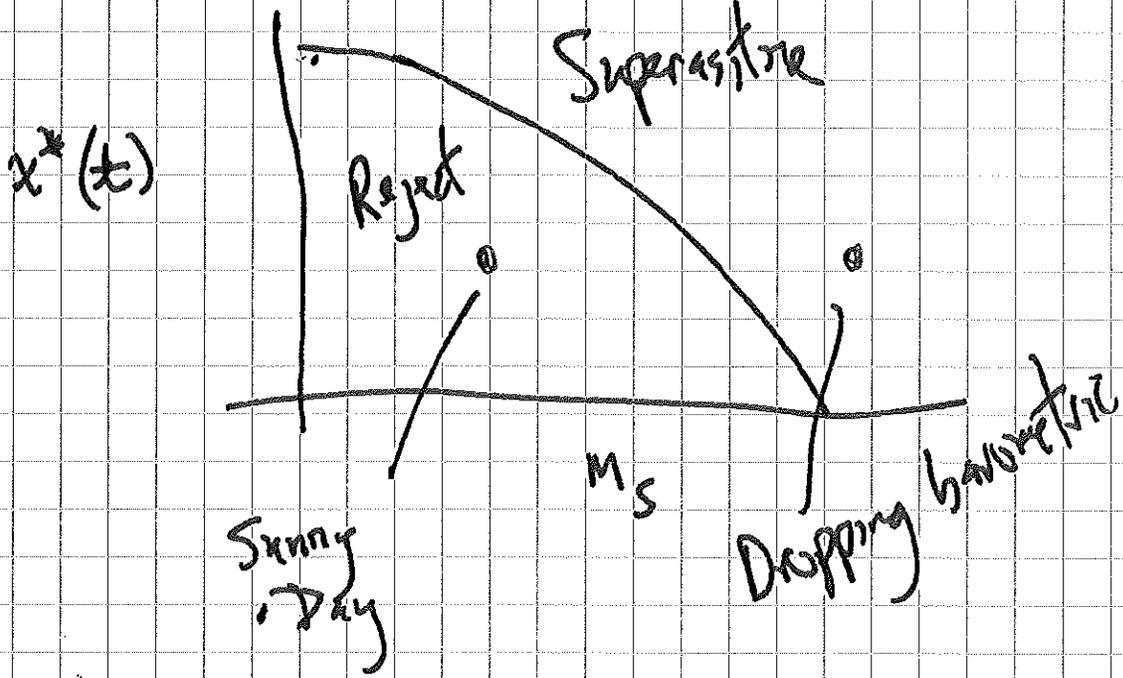
$$F(x, 1)$$

$$F(x, 1)$$



smallest
~~Time~~ Egg complement
at which she ~~is~~ is predicted to superparasitize





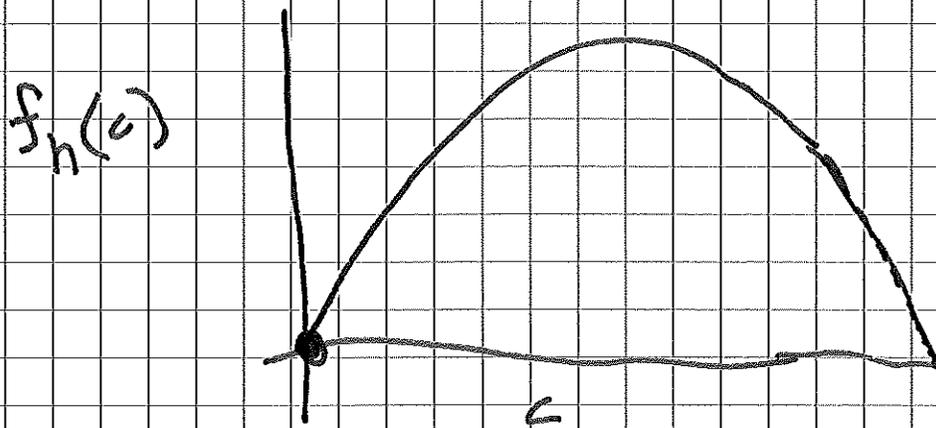
Univoltine, Proviogenic, Gregarious Parasitoid

17.9

H = # host types, characterized by

$\lambda_h = \frac{1}{\tau}$ { she encounters a host of type h in a single period of search }

$f_h(c) =$ Increment in lifetime accumulated fitness when she puts c eggs into a host of type h



- 2 lines
- Parabola
- Cubic

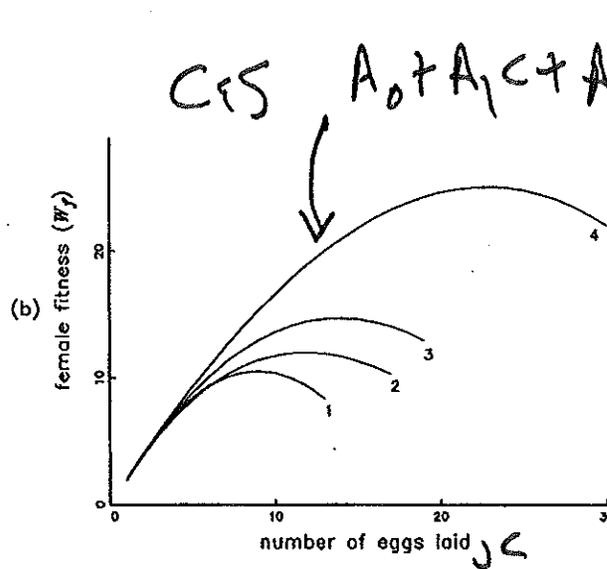
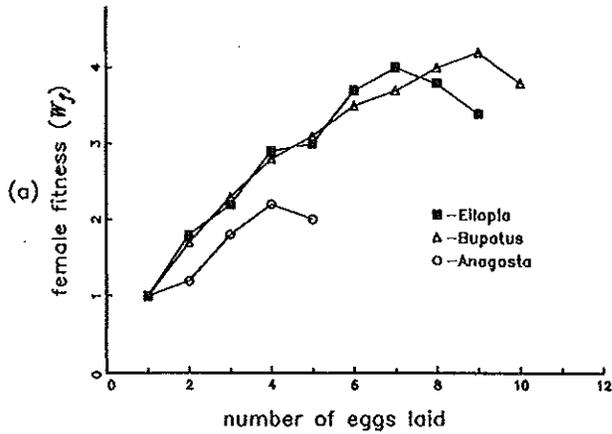
Young Man's favorite

$$f_h(c) = c \left(1 - \left[\frac{c}{c_{\max}(h)} \right]^{\gamma_h} \right)$$

$c_{\max}(h), \gamma_h \sim$ parameters

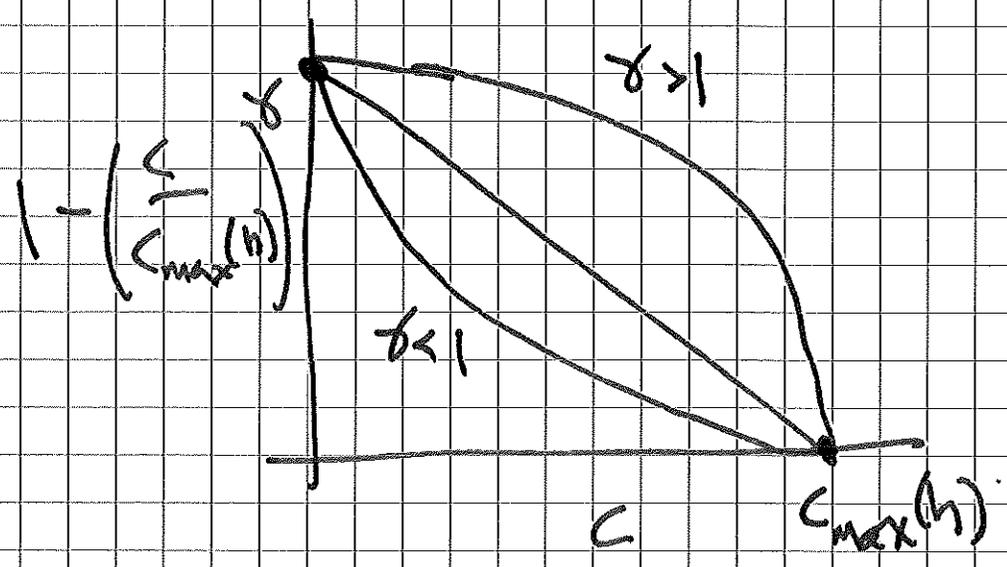
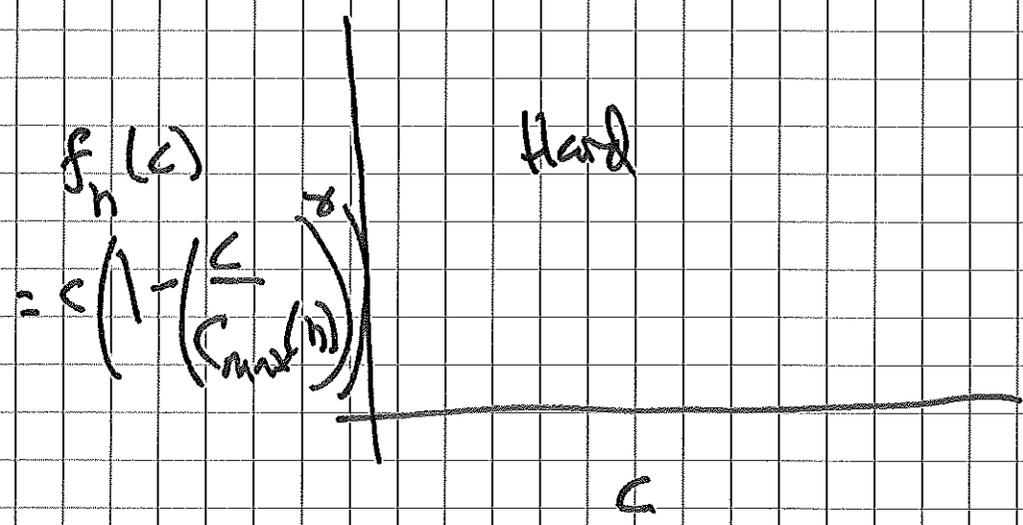
17.10

REPRODUCTION IN INSECTS ■ 129



Mangel and Clark
1988
Pg 128 for
values

Figure 4.1 Single host fitness increments computed by Charnov and Skinner (1984). (a) Fitness increments for the wasp *Trichogramma* on three different host types. (b) Fitness increments for the wasp *Nasonia* for four hosts of different volumes. (Redrawn from *Florida Entomologist* Vol. 67, 1984.)



Old Marc's Current Favorite

$$f_h(c) = c \left(1 - e^{-\delta_h (C_{max}(h) - c)} \right)$$

17.12

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

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

$$F(x, t) = \left(1 - \sum_{h=1}^H \lambda_h \right) e^{-m_s} F(x, t+1)$$

$$+ \sum_{h=1}^H \lambda_h \max_{c=x} \left[f_h(c) + e^{-(m_s + m_h \delta t)} F(x-c, t+1+\delta t) \right]$$

increase in
current reproduction

we could make this
fancier

$C_h^*(x, t)$
= optimal # of
eggs to lay in
a host of type
h when $X(t) = x$

22 April 2013

AMS 215: Important Dates and Deadlines

April 22 (midnight): Problems 3, 4, 5 due

April 24: No class (coding day)

April 26 (noon): Paper you like #2 in dropbox folder, report to Marc

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

May 6 (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}~~Kate~~, moderator).

May 15: No class (coding day); description of your project to Marc (midnight)

May 22: No class (coding day)

June 13 (midnight): Project reports/problems due

22.1

State-dependent habitat selection games between predators and prey: the importance of behavioural interactions and expected lifetime reproductive success

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845511

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ABSTRACT

The fitness of both prey and predators will be affected by the behaviour of conspecifics and other (predator or prey) species. However, little theory has considered the case where predators and prey respond to one another simultaneously. I present a framework that examines the impact of the predator–prey behavioural interactions (within and between species) in a state-dependent life-history context. I use multiple linked dynamic state variable game equations to predict the patch selection of prey and predators as a function of their energy reserves. When prey are expected to maximize their probability of survival, the individual predators and prey that are not at risk of starvation are predicted to be uniformly distributed among patches independent of the difference in resource input rates among sites. However, individuals near starvation cause more prey and predators to be found in high resource sites. In contrast, when predators and prey both maximize reproduction, predators and prey are predicted to show imperfect resource matching. The proportion of individuals at risk of starvation causes deviations from the perfect resource matching predicted by previous predator–prey games. The predicted patterns clearly illustrate the importance of recognizing that predators and prey will both respond concurrently to one another's distributions. However, the models also illustrate that an organism's state, competition among conspecifics and the life-history pattern of both predators and prey are key to understanding their distribution and behaviour. We can increase our understanding of these interactions and the distribution of predators and prey in space and time by combining the consideration of interactions within and between the species with knowledge of how foraging relates to lifetime expected reproductive success of both predators and prey.

Keywords: dynamic state variable model, game theory, habitat selection, life history, predator–prey interactions.

INTRODUCTION

Interactions between species are at the heart of many important ecological and evolutionary processes. Predator–prey dynamics are a classic and relatively well-studied example of

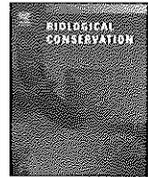
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Biological Conservation

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Use of patch selection models as a decision support tool to evaluate mitigation strategies of human–wildlife conflict

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Foraging theory

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Ursus americanus

ABSTRACT

Human-dominated landscapes offer spatially concentrated and reliable food resources that attract wildlife and lead to human–wildlife conflicts. Conflict management is often directed at humans (e.g., education) to reduce attractants, or foraging benefits to wildlife, or at wildlife (e.g., hazing) to increase foraging costs; but strategies can be expensive and ineffective. Because a key driver of conflict is the pursuit of food by wildlife, we used patch selection models, a dynamic, state-dependent modeling approach based on foraging theory, to assess how benefit reduction and cost increase resulting from conflict mitigation affect wildlife foraging decisions. We applied the patch selection models to a system in which American black bears (*Ursus americanus*) forage in urban and urban-interface patches and conflicts are common. We used survival as a fitness currency and body fat reserves as a state variable. We incrementally reduced availability of anthropogenic foods (benefit reduction) and increased energetic costs of movement in response to aversive conditioning treatments (cost increase) to search for thresholds resulting in avoidance of human-dominated patches. Benefit reduction $\geq 55\%$ in urban patches and $\geq 70\%$ in urban-interface patches resulted in avoidance by bears of almost all states. Cost increases achieving similar results exceeded 1100% and 400% in urban and urban-interface patches respectively, and are likely unrealistic to implement. Given modeling results and that control strategies targeting wildlife are unpopular with constituencies, we suggest allocating management resources to strategies that reduce availability of anthropogenic food.

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1. Introduction

Human–wildlife interactions, and subsequently conflicts, are increasing worldwide (Conover, 2001; Woodroffe et al., 2005). Human-dominated landscapes offer spatially concentrated, predictable, and reliable food sources, e.g., livestock, crops, or refuse, which can serve as major attractants to wildlife and lead to human–wildlife conflict (Shochat, 2004; Baker et al., 2008). Whether the resultant conflict occurs due to depredation of livestock in South America (e.g., Michalski et al., 2006), raiding of agricultural crops in Europe (e.g., Geisser and Reyer, 2004), or use of refuse in urban centers in North America (e.g., Beckmann and Berger, 2003), a key driver of conflict is the pursuit of food resources by wildlife. Thus, understanding how to best mitigate human–wildlife conflict requires an understanding of how management affects wildlife foraging decisions.

Two major management strategies aimed at humans and wildlife are commonly employed to resolve conflicts. Human-dimensions tools are implemented in conflict communities to change human behavior to reduce the availability of attractants, or foraging benefits, to wildlife. For example, improving husbandry through education reduced livestock depredation by snow leopards (*Panthera uncia*) in India (Jackson and Wangchuk, 2004), and proactively enforcing refuse disposal laws reduced availability of garbage to American black bears (*Ursus americanus*) in Colorado, USA (Baruch-Mordo et al., 2011). Wildlife management tools are also implemented to either eliminate (lethal control) or deter (non-lethal control) wildlife from attractant sites (Fall and Jackson, 2002; Treves and Karanth, 2003). Lethal control can be unpopular with wildlife managers (e.g., Fall and Jackson, 2002; Baker et al., 2005; Spencer et al., 2007), often motivated by the unpopularity of such management actions by the general public (Manfredo, 2008; Messmer, 2009). Therefore, wildlife agencies are increasingly using non-lethal aversive conditioning treatments, including hazing, and chemical or physical deterrents, with the goal of modifying the long-term behavior of wildlife due to the learning

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E-mail address: sbaruch-mordo@tnc.org (S. Baruch-Mordo).

22.3

Dear Marc,

Thank you very much for your feedback about the paper! It was fun to learn about the models (I thank Colleen Webb of Colorado State University for her excellent teaching), and apply them to a management question in my study area. And I'm thrilled that your students found it interesting and potentially helpful to their research! Definitely rewarding!

Thanks again!
Sharon

Sharon Baruch-Mordo
Spatial Scientist
The Nature Conservancy
sbaruch-mordo@tnc.org
<http://warnercnr.colostate.edu/~sharonbm/>

A STATE-DEPENDENT MODEL FOR THE OPTIMAL MANAGEMENT OF AN INVASIVE METAPOPULATION

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²Department of Biology, 208 Mueller Laboratory, The Pennsylvania State University, University Park, Pennsylvania 16802 USA

Abstract. Management of invasive species involves choosing between different management strategy options, but often the best strategy for a particular scenario is not obvious. We illustrate the use of optimization methods to determine the most efficient management strategy using one of the most devastating invasive forest pests in North America, the gypsy moth (*Lymantria dispar*), as a case study. The optimization approach involves the application of stochastic dynamic programming (SDP) to a metapopulation framework with different infestation patch sizes, with the goal of minimizing infestation spread. We use a novel “moving window” approach as a way to address a spatially explicit problem without being explicitly spatial. We examine results for two cases in order to develop general rules of thumb for management. We explore a model with limited parameter information and then assess how strategies change with specific parameterization for the gypsy moth. The model results in a complex but stable, state-dependent management strategy for a multiyear management program that is robust even under situations of uncertainty. The general rule of thumb for the basic model consists of three strategies: eradicating medium-density infestations, reducing large-density infestations, and reducing the colonization rate from the main infestation, depending on the state of the system. With specific gypsy moth parameterization, reducing colonization decreases in importance relative to the other two strategies. The application of this model to gypsy moth management emphasizes the importance of managing based on the state of the system, and if applied to a specific geographic area, has the potential to substantially improve the efficiency and cost-effectiveness of current gypsy moth eradication programs, helping to slow the spread of this pest. Additionally, the approach used for this particular invasive species can be extended to the optimization of management programs for the spread of other invasive and problem species exhibiting metapopulation dynamics.

Key words: decision theory; gypsy moth; invasive species management; *Lymantria dispar*; mainland-island metapopulation; optimization; stochastic dynamic programming (SDP).

INTRODUCTION

Biological invasions of pest species pose a threat to the stability of ecosystems, both natural and managed (Liebhold et al. 1995). Invasive species can alter habitats, through both direct and indirect competitive effects on other species, and can completely restructure a wide range of ecosystems (Mack et al. 2000). Additionally, invasive species are a threat to economics, societies, and ecosystems across the globe, costing countries billions of U.S. dollars per year in direct management costs in addition to the indirect costs of environmental damage, trade disruption, and disease risk (Global Invasive Species Programme 2005, Lodge et al. 2006). Because of the significance in both cost and ecological impact of invasive species, we are interested in determining the optimal management strategy for invasive species through the use of quantitative methods.

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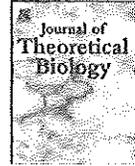
³ E-mail: tlb24@cam.ac.uk

Mathematical models, particularly optimization models, in conjunction with experimental research, can contribute to a more cost-efficient and practical approach to investigating and recommending management decisions for invasive species. Setting the stage, Moody and Mack (1988) developed a simple, one-time control model and found, for invasions radiating out of a few large, isolated infestations, it is best to control the smaller, satellite populations than the larger foci, contrary to typical management practice at the time. Their rule of thumb, to continually remove the small, new infestations, has been revisited by several recent studies (Taylor and Hastings 2004, Grevstad 2005, Hastings et al. 2006, Whittle et al. 2007). Most recently, Whittle et al. (2007) updated the original model and found a new optimal decision to focus on both the larger and satellite infestations, where the relative focus depends on the cost of managing vs. doing nothing. Using different quantitative methods, other studies have found modified optimal solutions including eradicating low-density (faster growing) subpopulations first, depending on the available budget (Taylor and Hastings 2004), attacking



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21.5

Physiological adaptations to climate change in pro-ovigenic parasitoids

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Egg load

Stochastic dynamic programming

ABSTRACT

Temperature increase can affect physiological and behavioural constraints. Here, we use a stochastic dynamic modelling approach to predict changes in physiological adaptations and behaviour in response to temperature increase of pro-ovigenic parasitoids (i.e., parasitoids that mature all of their eggs before emergence). Adults of most species of parasitoids, are not capable of *de novo* lipogenesis. The allocation of lipids accumulated during the larval stage determines adult lifespan and fecundity. In females, lipids can be allocated either to egg production or to adult lipid reserves leading to a trade-off between fecundity and lifespan.

Our results show that selection by an increase in ambient temperature, favours a smaller initial egg load and a larger amount of lipids for maintenance. The cost of habitat exploitation increases with temperature because the rate of lipid consumption increases. Hence, lifetime reproductive success decreases. When the optimal activity rate shifts to match the higher ambient temperature, these effects become less pronounced.

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1. Introduction

Levitus et al. (2001) estimate that the global mean temperature has risen by 0.6 ± 0.2 °C over the past century. In the near future, this increase in temperature is expected to accelerate. Some models predict that in the next decade global mean temperature will increase from 0.3 to 1.3 °C and temperate regions will probably experience a greater increase in temperature than tropical ones (Knutti et al., 2002; Stott and Kettleborough, 2002).

It is difficult to predict how animal populations might adapt to a warmer climate because an increase in temperature could lead to a shift in distribution pattern (Pearson, 2006; Peterson et al., 2002), to changes in phenology (reviewed in Visser and Both, 2005), and in adaptation of morphology, physiology and behaviour (Root et al., 2003; Walther, 2002; Hance et al., 2007; Gienapp et al., 2008). The evolutionary response of a species to a warmer climate will most likely include all of these, and investigation of each of these possible responses is needed for integrative predictions about the ability of animals to adapt to changes in climate.

Several studies have investigated the physiological and behavioural responses that individual organisms use to cope with an increase in temperature. Temperature increase may affect metabolic

and development rates (Huey and Kingsolver, 1989; Logan et al., 1976) or induce migration behaviour (Pearson, 2006; Peterson et al., 2002). Insect parasitoids are a useful biological model for investigating the effects of climate change on fitness, because their physiological and behavioural responses can easily be measured under laboratory conditions, and because there is a direct link between foraging behaviour and fitness. Moreover, adults of most parasitoid species, are incapable of *de novo* lipogenesis, and the allocation of lipids accumulated during the larval stage determines the budget for longevity and fecundity (Casas et al., 2005; Visser and Ellers, 2008; Visser et al., 2010). In females, lipids can be allocated to either egg production or stored as reserves leading to a trade-off between fecundity and longevity (Ellers and van Alphen, 1997; Pexton and Mayhew, 2002). Pro-ovigenic parasitoids, because they mature all their eggs during pre-adult development, are a suitable model to explore the effect of temperature on this trade off.

In response to an increase in average temperature, parasitoids could shift the trade-off between fecundity and longevity and adapt their rate of activity. The observation that ectotherms from temperate and tropical areas differ in thermal tolerance can be taken as evidence that natural selection has shaped activity patterns in relation to ambient temperature (Addo-Bediako et al., 2000; Deutsch et al., 2008). Like other ectotherms, parasitoids can adjust their activity rate as a function of temperature (Hance et al., 2007). As yet, no theory has been developed to predict how selection by a warmer climate would affect physiology and behaviour of parasitoids. Predicting such effects is not

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REVIEWS

Ways to test stochastic dynamic programming models empirically

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(Received 15 April 1999; initial acceptance 26 May 1999;
final acceptance 7 December 1999; MS. number: RV-17)

Stochastic dynamic programming (SDP) models are widely used to predict optimal behavioural and life history strategies. We discuss a diversity of ways to test SDP models empirically, taking as our main illustration a model of the daily singing routine of birds. One approach to verification is to quantify model parameters, but most SDP models are schematic. Because predictions are therefore qualitative, testing several predictions is desirable. How state determines behaviour (the policy) is a central prediction that should be examined directly if both state and behaviour are measurable. Complementary predictions concern how behaviour and state change through time, but information is discarded by considering behaviour rather than state, by looking only at average state rather than its distribution, and by not following individuals. We identify the various circumstances in which an individual's state/behaviour at one time is correlated with its state/behaviour at a later time. When there are several state variables the relationships between them may be informative. Often model parameters represent environmental conditions that can also be viewed as state variables. Experimental manipulation of the environment has several advantages as a test, but a problem is uncertainty over how much the organism's policy will adjust. As an example we allow birds to use different assumptions about how well past weather predicts future weather. We advocate mirroring planned empirical investigations on the computer to investigate which manipulations and predictions will best test a model.

© 2000 The Association for the Study of Animal Behaviour

Stochastic dynamic programming (SDP) is a computational technique that finds optimum sequences of actions. Since its promotion in behavioural ecology by McNamara & Houston (1986) and Mangel & Clark (1986), SDP modelling has been applied to a wide variety of phenomena, for instance: foraging (McNamara & Houston 1992); food caching (Lucas & Walter 1991); antipredation behaviour (Houston et al. 1993); intraspecific fighting and other games (Enquist & Lelmar 1987; Houston & McNamara 1988); movement and migration (Weber et al. 1998; Hutchinson 1999); mating tactics (Lucas & Howard 1995; Galvani & Johnstone 1998); and life history decisions about growth, reproduction and sex change (Iwasa 1991; McNamara & Houston 1996; Hutchinson et al. 1997). Mangel & Clark (1988) and Houston & McNamara (1999) provide further examples. One strength of SDP models is that they can be quite complex, yet computationally tractable.

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0003-3472/00/040665+12 \$35.00/0

The philosophy and aims of optimality modelling in behavioural ecology have been discussed elsewhere (e.g. Stearns & Schmid-Hempel 1987; Parker & Maynard Smith 1990). The purpose of some SDP models has been only to prove the logical coherence of verbal arguments. But often we want to test whether models fit observed biological phenomena. In this paper we aim to show that in this last respect SDP has not been used to its full potential. SDP can provide a variety of predictions that, if tested in combination, would yield more compelling evidence of whether a model is realistic.

SDP models have stimulated empirical experiments designed to test their predictions (e.g. Ekman & Hake 1990; Lucas & Walter 1991; Witter et al. 1995; Reinhardt & Healey 1999; Thomas 1999a, b). However, the number of parameters in some more realistic models can make them daunting to apply. Fortunately it is often unnecessary to know every parameter value accurately. Complex SDP models can produce simple predictions that are robust to a wide range of parameter values.

We start this paper with a nontechnical explanation of SDP models, including the definition of some standard

Effects of age- and state-dependent allocation on offspring size and number

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and Michael B. Bonsall³

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²*Center for Stock Assessment Research and Department of Applied Mathematics and Statistics, University of California, Santa Cruz, California, USA and*

³*Department of Zoology, University of Oxford, Oxford, UK*

ABSTRACT

Background: Empirical evidence from a range of taxa suggest age and condition can affect offspring size and number, but supporting theory is limited.

Question: How do age and condition influence offspring size and number?

Method: Dynamic state-dependent optimization.

Key assumptions: We model a capital-breeding life history where an individual matures with all reserves available for reproduction.

Results: We find that mortality risk and density-dependent offspring survival favour variation in allocation patterns. We predict that in species with sibling competition, females will reduce clutch size, but can compensate for fewer numbers of offspring with plasticity in offspring size and by reproducing several times over their life. In habitats with low mortality risk and some sibling competition, we predict an increased optimal offspring size in larger and older females.

Keywords: density dependence, inter-generational transfers, life-history plasticity, maternal age, maternal effect, state dependence.

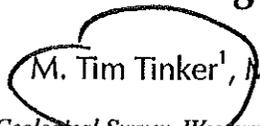
INTRODUCTION

Theory aimed at predicting maternal allocation of resources to clutch size and offspring size has historically considered these traits independently. As a result, life-history predictions generally follow from two well-developed lines of thinking about allocation to reproductive traits. The first, the dynamics of offspring number, is the study of how limited resources of fixed size (eggs or larvae) are predicted to be distributed over time in response to ecological and physiological conditions. The formal study of the dynamics of offspring number

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Learning to be different: acquired skills, social learning, frequency dependence, and environmental variation can cause behaviourally mediated foraging specializations



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¹US Geological Survey, Western Ecological Research Center, Long Marine Laboratory, Santa Cruz, California, ²Center for Stock Assessment Research, Department of Applied Mathematics and Statistics, University of California at Santa Cruz, Santa Cruz, California and ³Department of Ecology and Evolutionary Biology, University of California, Center for Ocean Health, Santa Cruz, California, USA

ABSTRACT

Question: How does the ability to improve foraging skills by learning, and to transfer that learned knowledge, affect the development of intra-population foraging specializations?

Features of the model: We use both a state-dependent life-history model implemented by stochastic dynamic programming (SDPM) and an individual-based model (IBM) to capture the dynamic nature of behavioural preferences in feeding. Variables in the SDPM include energy reserves, skill levels, energy and handling time per single prey item, metabolic rate, the rates at which skills are learned and forgotten, the effect of skills on handling time, and the relationship between energy reserves and fitness. Additional variables in the IBM include the probability of successful weaning, the logistic dynamics of the prey species with stochastic recruitment, the intensity of top-down control of prey by predators, the mean and variance in skill levels of new recruits, and the extent to which learned information can be transmitted via matrilineal social learning.

Key range of variables: We explore the effects of approaching the time horizon in the SDPM, changing the extent to which skills can improve with experience, increasing the rates of learning or forgetting of skills, changing whether the learning curve is constant, accelerating ('J'-shaped) or decelerating ('r'-shaped), changing both mean and maximum possible energy reserves, changing metabolic costs of foraging, and changing the rate of encounter with prey.

Conclusions: The model results show that the following factors increase the degree of prey specialization observed in a predator population: (1) Experience handling a prey type can substantially improve foraging skills for that prey. (2) There is limited ability to retain complex learned skills for multiple prey types. (3) The learning curve for acquiring new foraging skills is accelerating, or J-shaped. (4) The metabolic costs of foraging are high relative to available energy reserves. (5) Offspring can learn foraging skills from their mothers (matrilineal social

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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

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

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

Dependent young

Learning

Patch depletion

Schooling behavior

Spatial structure and networks of patches

Games against conspecifics

Predator-prey games

Prologus, Bergman, and the Parasitoid

22.16

$$F(x,t) = \max E \left\{ \text{accumulated fitness} \right. \\ \left. \text{from oviposition between } t \text{ and} \right. \\ \left. T \mid X(t) = x \right\}$$

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

egg oviposited at time t

$$F(x,t) = \left(1 - \sum_{h=1}^H \lambda_h \right) e^{-m_s} F(x,t+1)$$

$$+ \sum_{h=1}^H \lambda_h \max_{c \leq x} \left[f_h(c) \right. \\ \left. + e^{-m_s - m_o \tau} F(x-c, t+1+\tau) \right]$$

current clutch

Pseudo Code

Do the preliminaries

 $c^*(x, h, t) =$ ~~opt~~ optimal clutch when she encounters host type h with $X(t) = x$

Loop Over Time

Loop Over x

$$\text{Set } F(x, t) = \left(1 - \sum_{h=1}^H \lambda_h\right) e^{-\lambda_h x} F(x, t+1)$$

Loop over h

$$\text{Set } V_{\max} = 0$$

Loop Over ~~0~~ $0 \leq c \leq x$

$$V_{\text{test}} = f_h(c)$$

$$+ e^{-\mu_h - \mu_d t} F(x-c, t+(t+1))$$

IF $V_{\text{test}} > V_{\max}$

$$\text{Set } V_{\max} = V_{\text{test}}$$

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

Next c

$$\text{Replace } F(x, t) \text{ by } F(x, t) + \lambda_h V_{\max}$$

Next h Next x Next t

egg complement-time boundary for super-parasitism and then explore how that boundary changes as you vary one of the parameters. Does the result correspond to your intuition. Limit yourself to 5 pages. Due 6 May

Problem 7 Code the model for the univoltine, gregarious, pro-ovigenic parasitoid that we developed in class, assuming three host types. You can begin with the equation, but should explain your choices for the various parameters that go into the model. Once you have coded the backward part, write a forward simulation mimic the experiments of Rosenheim and Rosen. Limit yourself to 5 pages. Due 6 May

Solitary

$$f_p, f_u$$

T

$$m_s, m_o$$

γ

$$X_{max}$$

~~$\lambda_1, \lambda_2, \lambda_3$~~

$$g_p, g_u$$

Gregarious

$$f_1(c), f_2(c), f_3(c)$$

T

$$m_s, m_o$$

γ

$$X_{max}$$

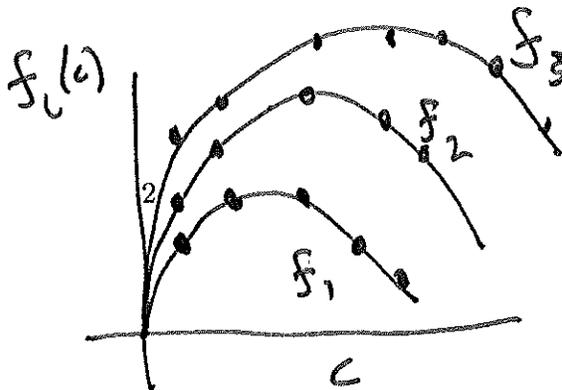
$$\lambda_1, \lambda_2, \lambda_3 \geq 0$$

$$\lambda_1 + \lambda_2 + \lambda_3 \leq 1$$

$$0 < f_p < f_u$$

$$0 < g_p, 0 < g_u$$

$$g_p + g_u \leq 1$$



$$e^{-m_s T} = \underbrace{(e^{-m_s}) (e^{-m_s}) \dots (e^{-m_s})}_{T \text{ times}}$$

\uparrow
 $\equiv \text{Pr}\{\text{she survives to time } T \text{ given only trading}\}$

For beginners: Make this $\approx 1\%$

\downarrow
 \leftarrow Don't make this too small //