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Event-driven competing risks

Bland Ewing [a], Brian S. Yandell [b,1,*], James F. Barbieri [c,d], Robert F. Luck [c], Lisa D. Forster [c]

[a] *Department of Entomology, University of California, Berkeley, CA, USA*
[b] *Departments of Statistics and Horticulture, University of Wisconsin-Madison, 1210 West Dayton Street, Madison, WI 53706-1685, USA*
[c] *Department of Entomology, University of California, Riverside, CA, USA*
[d] *Advanced Systems Development, NAWC-WPNS, China Lake, CA, USA*

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Abstract

The California red scale *Aonidiella aurantii* (Maskell) (Homoptera: Diaspididae) is a major pest of California citrus, with infestations causing growers significant financial losses. It has recently developed resistance to traditional insecticide sprays. An alternative suppression tactic is the release of a biological control agent, *Aphytis melinus* DeBach (Aphelinidae: Hymenoptera) that feeds on red scale. Although many aspects of the red scale–*Aphytis* interaction are now understood, it is difficult to differentiate the effects of temperature and population fluctuations in the field. To investigate such complex interactions, we propose a new stochastic modeling technique, based on event-driven competing risks, that incorporates details of life histories as well as the host–parasitoid interaction. Our continuous-time, individual-oriented modeling approach quantifies relationships among individuals and describes the resulting coupling between the interacting populations. The event-structured simulation drives time in contrast to the usual time-driven stochastic dynamic programming. Our system, developed in the public domain using the R statistical package, allows for different biological clocks, since both red scale and *Aphytis* development respond to temperature (degree-days) while searching female *Aphytis* follow a diurnal time schedule, contingent upon temperature-dependent egg maturation.

Keywords: Discrete event system; Stochastic Petri net; Individual-oriented model; Stochastic dynamic programming

1. Introduction

Stochastic models in ecology attempt to incorporate key underlying processes of an ecological system, allowing the study of multiple realizations through simulation. We focus here on models of life history events for interacting populations. The life table approximation of dividing time into

* Corresponding author. Tel.: +1-608-262-2598; fax: +1-608-262-0032
E-mail address: yandell@stat.wisc.edu (B.S. Yandell).
[1] www.stat.wisc.edu/ ~ yandell/ewing

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discrete "quanta" migrated early into stochastic models in ecology. Modern ecological simulation studies consider ever smaller time increments using this same fixed time step framework (Mangel and Clark, 1988; Wolff, 1994; Hutchinson and McNamara, 2000). While finer scale increments can capture more intricate events, they require more time simulating null activity. Further, their discrete nature can introduce unintended artifacts that are difficult to unravel.

Work in complexity (Langton, 1986) suggests that higher level structure can emerge from self-organizing processes occurring at lower levels. However, such models to date suffer from the same quantization problem found with life-table derived methods. Recently, Gronenwold and Sonnenschein (1998) used cellular automata based on Petri nets to model a host–parasite interaction. Unfortunately, efforts to globally synchronize their model to reflect annual cycles introduced unacceptable network complexity. Such synchronized models cannot detect emergent patterns.

Alternatively, we propose to base models on the actual time of events. The difficulty with this shift in perspective is that events for individuals are no longer synchronized, making life table and generation summaries problematic. The development below of a simulation structure for competing risks in a biological system is built upon the concept of potential lifetimes using the cumulative risks as a basic building block. This approach uses detailed knowledge of the biological system under study, providing a framework to incorporate known and suspected aspects of that system. Our approach has close connections to continuous-time stochastic Petri nets (Ajmone Marsan et al., 1995; Lindemann, 1998) that are event-driven. However, we believe our perspective offers a much simpler way to develop ecological models, focusing on the next scheduled event and the local structure of competing risks for event transitions.

The study of any biological system is intrinsically dependent on the choice of measurements and the manner of sampling. Typically, a sample of members of a population is observed with each individual viewed as an integral organism functioning as a single unit, albeit interconnected to others. Activities of these individuals are recorded in terms of life history events described at some resolution of time, space and detail depending on the purpose of the study. Observations measured over some span of time and space form the basis for understanding the biological system. We can develop a model framework directly driven by these measurements.

We first consider a living system as a stochastic process, recasting concepts of events for an individual and a population of individuals in a biological system. We then detail the biology of the red scale/*Aphytis* host–parasitoid system to identify features of life histories and inter-species interactions important in simulation. We develop a competing risks framework with attention to modeling an individual's biological clock in a simple but effective manner. Finally, we show initial results of our red scale/*Aphytis* ecosystem simulation.

2. Event-driven considerations for living systems

Consider a living system as a complicated stochastic process X that progresses through time from one event to the next. An *event* is defined as a significant biological change that can be marked and counted, resulting in an instantaneous state change. That is, at time t the process changes state to $X(t) = s$. The composite state s may be rather intricate, specifying the state of every individual in the system explicitly or implicitly. Stochastic processes are usually described as time-driven. This has led to a whole simulation industry in stochastic dynamic programs (Hutchinson and McNamara, 2000), stepping through finer and finer time increments to approach "reality".

Imagine a living system as a sequence of events, beginning in state s_0 at time $t_0 = 0$, with events, or state transitions, $s_0 \to s_1 \to s_2 \to \cdots$ and event times $t_1 < t_2 < \cdots$. If the structure of the system does not change, events can be scheduled as far forward as desired. However, a change in state may alter the entire state space for the future of the stochastic process. Thus X actually depends on both time t and the current state s. Imagine a progression of stochastic processes indexed by the current state, $\{X(t,s_k), t > t_k\}$, $k = 0, 1, \ldots$, with s_0

the initial state at $t_0 = 0$ and s_k the current state after the future event at time t_k. The realization of this stochastic process is equivalent to a sequence (t_0, s_0), (t_1, s_1), …, (t_k, s_k), etc. While this can theoretically be accommodated within the framework of semi-Markov processes by extending the sample space to be arbitrarily large, it provides little insight into how to implement a simulation in practice. Even for small simulations, this structure can become cumbersome and expensive, as the occurrence of each event requires rebuilding the entire event space.

Think of a living process as moving from event to event, with time defined implicitly through the sequence of realized events, yielding a practical construction of simulations. That is, if the current state s_1 was realized at time t_1, then the future event $s_1 \to s_2$ could happen at some random future time $t_2 = T(s_1 \to s_2 | t_1, s_1)$. This property allows a smooth transition between the time domain of the biological system and the event domain in modeling the biological system.

The investigator decides up front the aspects of a biological system to be studied based on measurable events and the focus of scientific inquiry, implicitly setting the resolution and span of the model. *Resolution* is the smallest increment of time and space that contributes useful biological information, with events over smaller scales assumed to occur instantaneously. A finer scale model would increase the cost of simulation while providing negligible insight. *Span* is the largest amount of time and space the model can encompass, with aspects occurring over longer intervals considered as essentially constant or slowly varying in a smooth fashion. Changing the resolution and span of a model profoundly affects what features of a biological system can be studied, and vice versa. For example, an *Aphytis* parasite feeding on California red scale would appear to be instantaneous with a resolution of minutes, but would require detailed modeling with a resolution of seconds. A mature orange fruit could be considered static as a substrate for red scale over a span of 6 months. It may be appropriate to model at several different spatial and temporal spans and resolutions to address different facets of a biological system.

We can schedule the next event for every individual in a population. However, individuals may interact, in some cases leading to births or deaths that can change the structure of the system. We define three special types of events to address these contingencies:) >

1) *Future events* are events that are scheduled to occur at some future time based on the competing risks system. Examples include reproduction and developmental stage transitions.
2) *Immediate events* handle multiple events that are not resolved individually at the resolution of the simulation. Such events—the birth of multiple offspring—appear to be coincident.
3) *Pending events* are events whose occurrence depend conditionally on other events or particular states of the model. This is especially designed to deal with predators and prey, or parasitoids and their hosts. It can also address events that depend on environmental changes such as rainfall and fire.

It is helpful to draw connections to Petri nets (cf. Ajmone Marsan et al., 1995; Lindemann, 1998), which put equal emphasis on states (places) and events (transitions) connected by arcs. Future events are instantaneous transitions from places that have continuous, stochastic delay times. Individuals (tokens) are reserved for an instantaneous transition by the scheduling of a future event; for instance, an insect scheduled to molt between instar stages. Future events may involve a stochastic choice among several competing risks, such as whether to feed or lay eggs, whether to search for food or move. Competing risks are analogous to race policies for conflicts in Petri nets, although our emphasis is on modeling the stochastic decision process itself.

Reproduction is a future event that may result in the birth of offspring. These births may be considered as immediate events with multiple arcs emerging from the birth transition. All arcs are followed, and hence all such immediate events are realized. These are sometimes described as deterministic events in Petri net literature. Typically immediate events result in scheduling of

several future events. For instance, birth brings new individuals into the simulation, each having scheduled future developmental transitions.

Death is often a pending event, since it may hinge on locating and consuming an adequate amount of resources while avoiding predation. We focus on "finding food" rather than "food availability", modeling the process of obtaining a resource as well as its presence. Pending events depend conditionally on other events and on the model state, such as cooperation among individuals for group hunting or germination of fire-sensitive seeds. Pending events are not scheduled in advance, avoiding the need for a complicated competing risks structure involving groups of individuals. Instead, pending events are interruptions to individual life histories arising from environmental changes or events involving other individuals. We represent pending events by dashed arcs to distinguish them from future events. If an individual is interrupted by parasitism, the pending event of being parasitized is realized. The individual may be killed or hurt in some way, depending on the nature of parasitism, canceling or altering its previously schedule future event.

3. The red scale/*Aphytis* system

In California, red scale, *Aonidiella aurantii* (Maskell) (Diaspididae: Homoptera) is a major insect pest of citrus, especially in California's San Joaquin Valley where most of the State's citrus is now grown. At moderate densities, the scale infests the fruit, while at higher densities they cause leaf and twig death, which can reduce fruit production. Dense scale populations can kill branches or portions of the tree with the subsequent loss of all or part of the crop. California's citrus is marketed as fresh fruit. Fruit with scale are downgraded or culled and most culled fruit are juiced, which does not cover production and processing costs. Thus, marketing conditions make cosmetic damage economic.

Growers in the San Joaquin Valley traditionally suppressed scale infestations with broad-spectrum insecticides. Recently red scale has evolved resistance to these pesticides, making them ineffective (Grafton-Cardwell, 1994). An alternative suppression tactic employs the release of a small wasp, *Aphytis melinus* DeBach (Aphelinidae: Hymenoptera). *Aphytis* parasitizes specific stages of the scale insect to produce its offspring, killing the scale as a consequence. When sufficient scales are parasitized, the scale population is suppressed at densities below those of economic concern. Release of this wasp in the absence of broad-spectrum insecticides can suppress the scale at a cost equal to or less than that achieved with the traditional insecticide program. Moreover, the quality of the fruit harvested under such a program is equal to or better than that harvested under the traditional program. (Haney et al., 1992; Luck et al., 1997).

3.1. Red scale life history

Red scale's life cycle begins with the crawler stage, a brief mobile stage that allows the young scale to find a suitable location on a branch, leaf or fruit on which to "settle". It then inserts its mouthparts into the substrate and transforms into a sedentary feeding stage. Once settled, a female scale remains immobile for the rest of her life. In contrast, the male once settled remains immobile until its adult stage when it transforms into a winged adult and seeks a virgin female with which to mate. Both the male and female grow by molting periodically, alternating between a feeding instar and a non-feeding or molting stage. During the molting stage, the scale sheds its exoskeleton and increases its size so that it can grow when it initiates feeding during the next instar. A female red scale has three feeding stages (instars) with two intervening molts. At the end of the third instar, it mates and transforms into a gravid female, maturing its eggs, and subsequently produces crawlers. The eggs develop within the female. Immature males have two feeding instars separated by a molt stage. Following the second molt, the male transforms into a prepupa followed by a pupa, finally emerging as a winged adult. The winged adult locates a virgin female with whom to mate via a sex pheromone. This is illustrated in Fig. 1.

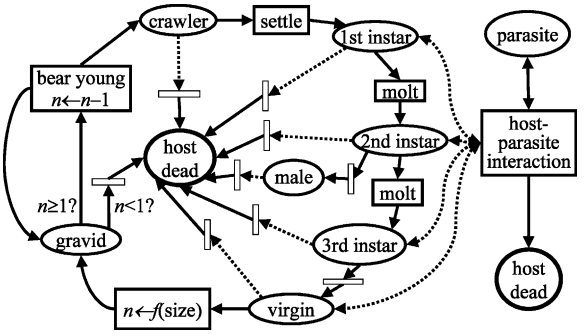

Fig. 1. Red scale life history. Red scale remains in a particular state (ellipse) for a scheduled period of time measured in degree-days (see text), and then experiences an event (rectangle) that moves it to the next stage. Some labeled rectangles represent complicated processes such as host–parasite interaction that may take time to be realized. Arcs connect events to states and vice versa. Dashed arcs indicate interruptions, for instance parasitism, or death due to some unknown cause. Gravid females have some reservoir n of potential young based on their size, which is depleted each time they bear a crawler until they finally die. Bearing young may involve time delays. Settling of crawlers is not detailed here.

Since red scale's development is temperature-dependent, the average time it takes the scale to complete its development during an instar or molt is represented in degree-days (DD°), which are approximately the cumulative degrees (°C) above 11 °C (Yu and Luck, 1988). It takes both female and male scales about 183 DD° to reach the end of the second instar. Males remain prepupae for an additional 17 DD° before molting to a pupa, and, after 11 DD° as a pupa, emerge as a winged adult. In contrast to males, second instar females, on the other hand, molt, which last approximately 28 DD° after which they reinsert its rostrella and feed as third instars. Red scale is subject to parasitism during the development process, until it becomes a mature adult. A mated female becomes attached to her scale cover and begins to mature her eggs. In approximately 50 DD°, the mature female begins to produce crawlers. The cycle for a female from crawler to crawler producing female takes approximately 360 DD°.

3.2. *Aphytis* life history

A. melinus is a small wasp that lays its eggs externally on the body of red scale (=host) but beneath the scale cover (Forster et al., 1995). It paralyzes the scale before it lays its egg. Normally, *Aphytis* lays its egg on a second or a third instar female or on a second instar male scale. *Aphytis* prefers instar stages to molt stages of red scale. During the instar stage, the scale cover is free of the body and *Aphytis* can lay eggs on either or both the dorsal and ventral surfaces of the scale (Abdelrahman, 1974; Luck et al., 1982). During the molt and mature female stage, the cover is rigidly fused to a hardened body. The wasp larva hatching from the egg feeds on the paralyzed scale, consuming the contents of the scale, which kills it. This is referred to as parasitization. The food available to the developing *Aphytis* is determined by the size of the scale body at the time the scale is paralyzed. *Aphytis* passes through four immature stages during its development: egg, several larval stages, prepupa and pupa. Generally, *Aphytis* allocates a male offspring on second instar scales and on male and female scales. About 20% of the male scales are allocated a female *Aphytis*. About 70% of the third instar female scales are allocated a female *Aphytis* offspring, about 25% are allocated a male *Aphytis* offspring and about 5% are allocated two *Aphytis* offspring (usually a male and a female) (Luck et al., 1982; Luck and Podoler, 1985). The two eggs are laid during the same host visit and represent a case of gregariousness (Luck et al., 1982).

Once having allocated an offspring to a host scale, the *Aphytis* egg or larva is vulnerable to usurpation of the host by a second female *Aphytis* encountering the host. A previously laid *Aphytis* egg or the first instar larva arising from it may be killed when a second female encounters and oviposits on the previously parasitized host (Forster and Luck, pers. obs.). The second female distinguishes the scale as previously parasitized and, while walking on the scale cover or probing the scale, detects chemical cues that were left by an *Aphytis* that previously oviposited on the scale (van Lenteren and DeBach, 1981). It punctures the previously laid egg and then lays its egg on the host, usurping the scale as a resource for its offspring (=super-parasitism) (Forster and Luck, pers. obs.). This usurpation increases in frequency as the ratio of unparasitized to para-

sitized scales decreases. This form of intraspecific competition can occur more than once on a host but, with each usurpation, the survival of the wasp larva arising from each newly laid egg decreases.

A. melinus development is also temperature-dependent. At 26.7 °C, in a parasitized or super-parasitized host, a wasp egg hatches after about 2 days. The resulting larva feeds for approximately 5 days before becoming a prepupa for 1 day. It pupates for 4–5 days before chewing a hole through the scale cover and emerging as an adult *Aphytis*. Thus, the entire process from egg to adult takes 12–13 days. *Aphytis* prefers instar stages to molt stages of red scale. During the instar stage, the scale cover is free from the body. The development of *Aphytis* is illustrated in Fig. 2, while parasitism is shown in Fig. 3.

Female *Aphytis* usually mature their first batch of eggs, approximately 12% of its lifetime egg supply, within 24 h of emergence using resources from their larval stage. They produce eggs during their entire adult lifetime, relying on periodic feeding on body fluids of small, immature hosts for sustenance (Opp and Luck, 1986; Heimpel and Rosenheim, 1998; Collier, 1995; Luck and Nunney, 1999). Adult *Aphytis* host feed by probing the scale body more extensively than when they oviposit, feeding on the body fluids that ooze from the wound. *Aphytis* feed on small hosts

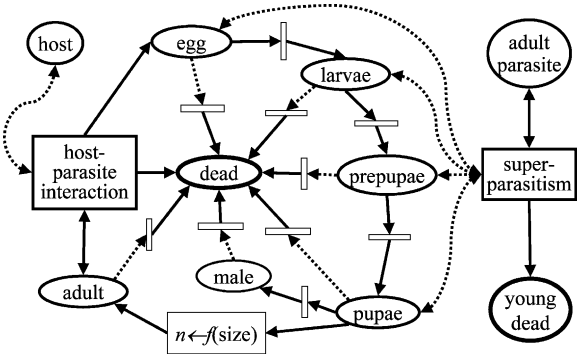

Fig. 2. *Aphytis* life history. All stages but the adult occur within a parasitized red scale host. A parasite may be displaced by a subsequent parasitism event. See Fig. 1 for details on symbols.

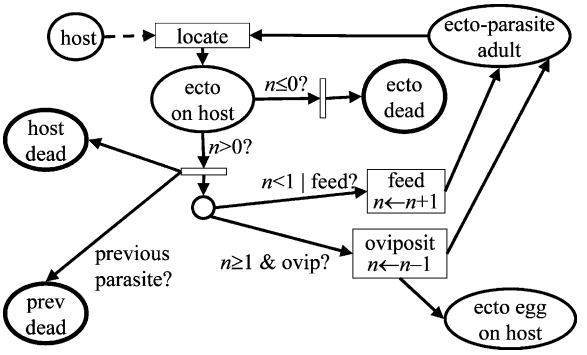

Fig. 3. Host–parasite interaction for ectoparasite, including super-parasitism. Parasite stops host development and kills any other parasite, including its own species that may be residing on the host. Parasite continues to locate new hosts until its reservoir (n) is depleted. Locate process is not detailed here. Choice of feed or oviposit depends on n and on the size of the selected host, which may also affect the probability of a male parasite egg.

(scales) while searching for larger scales to serve as suitable hosts on which to lay eggs. Host feeding kills a substantial percentage of California red scale beyond those killed through parasitism. Within 12–18 h of host feeding, the female develops approximately 1.3 eggs if it has not recently oviposited, or about 2.7 eggs if it has. Host feeding appears to provide resource for both metabolic maintenance and egg production. Collier (1995) showed that *Aphytis* that do not have access to hosts for either oviposition or host feeding will reabsorb about 1 egg per day. However, egg reabsorption will not supply the metabolic needs of the wasp in the absence of honey or other carbohydrates.

Aphytis, as with most parasitoids, controls the sex of its offspring by optional fertilization of eggs: males normally arise from unfertilized eggs while females arise from fertilized eggs (Yu and Luck, 1988; Godfray, 1994). Larger scales are allocated female eggs as large daughters are more reproductively successful on average than a smaller daughters. Thus scales growing on fruit are more likely to be parasitized due to their larger size (Luck and Podoler, 1985; Hare and Luck, 1991).

4. Competing risks for life events

Competing risks arose initially in mortality studies of risks that "compete" for an individual's life (Chiang, 1968, 1972). Competing risks and related life table methods have been used regularly in ecological modeling (Caswell, 1989), usually with discrete, synchronized generations. Here we adapt the building blocks of competing risks to study life history events for asynchronous, interacting individuals in an ecological community. We show how the linear structure of competing risks over continuous-time allows a simple modeling approach, as we only need to examine the next scheduled event in an ecological community. In addition, we introduce a parameterization of the cumulative risk, or mean value function, that allows quick adjustment of individual biological clocks.

While the competing risks literature has largely focused on inference (cf. Fine, 1999), we concentrate on simulation models grounded in measurable events. Fix and Neyman (1951) introduced an illness-death process, generalized by Chiang (1968), with individuals moving between healthy and sick states, continually exposed to competing risks of death. Clifford (1977) proved the non-identifiability of competing risks with a single measurement per individual even if an illness is progressive. Yandell (1982) showed that independent competing risks can only be identified with measurements at the actual times of transition between states. Thus, it is crucial to select events whose time of occurrence can be estimated. Simulation models should reflect this constraint.

The ethologist tries to define the probabilities for each event to reflect the observed data. Since events contain all the measured dynamics for the population; there is an added advantage in modeling simulations from the event domain. Future events change time in the model and control the competing risk sequencing. When a future event occurs, the simulation stops. Action is taken on any immediate events induced by the future event, and any pending events are modified as necessary. Immediate or pending events can change the underlying structure of the model, requiring the rebuilding of the stochastic process. In most situations, only a few competing risks are altered by the immediate or pending events, requiring only modest changes to other scheduled future events. Finally, the stochastic process is reconstructed to contain only future events from the current time onward.

Thus a biological system can be simulated by alternating between future events and immediate events, addressing pending events as they arise. However, the competing risks structure for future events now depends on the past history of events. Risks may be altered by discrete state changes of other individuals or by discrete or gradual changes in environmental conditions. Nevertheless, the stochastic process is still predictable and hence is still well defined.

4.1. Competing risk structure

An individual in an ecological community has several "choices" about future events, such as dying from one of several competing reasons, eating, reproducing, or migrating to another locale. The chance of the jth type of event occurring during the time instant t is proportional to its competing risk, or hazard, $m_j(t)$, which may change over time but is assumed to be fairly well behaved. We assume the probability of two or more events occurring simultaneously is negligible. Thus the risks add up to the chance of *any* event in an instant as $m(t) = \Sigma m_j(t)$. The cumulative competing risks, or mean value functions $M_j(t) = \int m_j(t)\,\mathrm{d}t$ with $M_j(0) = 0$, count the expected number of events of type j up to time t. These are assumed to be right-continuous and non-decreasing with derivative $m_j(t)$ at all but a countable number of time points. The random count of the number of events over time is a non-homogeneous Poisson process with time-varying risks and independent increments between distinct time intervals.

An alternative approach models potential life (or event) times T_j for each type of risk j (cf. David, 1974). The observed time to next event would be the minimum of these potential event times, $T = \min\{T_j\}$. Hence, the chance that no event occurs before time t is

$$\Pr\{T > t\} = \Pr\{\min(T_j) > t\} = \prod \Pr\{T_j > t\}$$
$$= \prod \exp(-M_j(t)) = \exp\left\{-\sum M_j(t)\right\}.$$

The product $\prod$ is justified if the potential event times, or equivalently the competing risks, are independent. The linearization property reduces a potentially complicated probability to a summation over the competing risk structure. Tsiatis (1975) showed that without independence T_j, and hence $M_j(t)$ and the sub-probabilities $\Pr\{T_j > t\}$, cannot be uniquely determined from the data. Further, it is impossible to investigate this assumption of independence with these data; as a result, these potential lifetimes have fallen out of favor. While we agree that inference cannot be based on these potential event times, they can be extremely useful for simulation models of complex living systems.

Each individual i has a set of potential times $\{T_{ij}, j = 1, 2, \ldots\}$ for its future events. These may depend on the history and current state of the biological system. Its next future event is at the minimum $T_i = \min\{T_{ij}\}$. The next event in a community of n individuals occurs at the minimum over all individuals, $T = \min\{T_i, i = 1, \ldots, n\}$. In a simulation with a high degree of structure and many levels of events, this minimization property provides an efficient method to find the next event for the community. Note that the mean number of events for a community is the sum $M(t) = \Sigma M_i(t)$, with the mean number for individual i being $M_i(t) = \Sigma M_{ij}(t)$. That is, the competing risk structure until the next future event decomposes in this linear fashion as if the individuals were independent.

4.2. Time depends on events

Control over the shape of the mean value functions M allows considerable flexibility to incorporate relevant knowledge of biological processes into the distribution of the scheduling time T. The mean value function M could be "estimated" from prior experimental data, partial knowledge and hunches. We show in this section how to schedule future events by drawing uniform or exponential random numbers and using M to transform to future event times.

Consider a single individual and a single competing risk, dropping subscripts for now. We can schedule the time T for its next future event by picking a random probability U, uniform between 0 and 1, and defining time T in terms of U as $M^{-1}(G(U)) = T$ with $G(u) = -\log(1-u)$ and M^{-1} the (generalized) inverse of M. Thus

$$\Pr\{U = u\} = u = 1 - \exp(-M(t)) = \Pr\{T = t\}$$

with some adjustment necessary for the chance $\Pr\{T = \infty\} \geq 0$ that no event occurs. Hence, time T becomes an implicit, dependent variable, driven by the event structure embodied in M. Fig. 4 shows this mapping for a distribution that has a plateau in the middle.

The random variate $V = G(U) = M(T)$ has a standard exponential distribution $\Pr\{V = v\} = 1 - \exp(-v)$. If the risk is constant, $m(t) = c$, then $T = V/c$. Sampling V instead of U involves only modest extra work (Ahrens and Dieter, 1974, 1988) and avoids calculating logs, which are expensive computationally. Events may, therefore, be scheduled by sampling a standard exponential random variable V and constructing the random time T as $M^{-1}(V) = T$ using the fact that $\Pr\{V = M(t)\} = \Pr\{T = t\}$. Thus, the mean value function M transforms the exponential waiting time V based on constant risks to a biological time that may encompass the ongoing processes of the simulated ecosystem (see Fig. 4).

4.3. Event structure for an individual

This generic mean value function M must be fine-tuned to each individual in a species, and to different species in a community. Future event times may need to be adjusted based on the individual histories and situations. In practice, many individuals may have similarly shaped mean value functions for a given competing risk. Changes during the simulation may slow or delay each biological clock, or increase the risk of certain types of events. Thus it is feasible to design a few such curves and then shift, stretch or otherwise modify them to suit multiple needs. This can enhance the biologist's control over model simula-

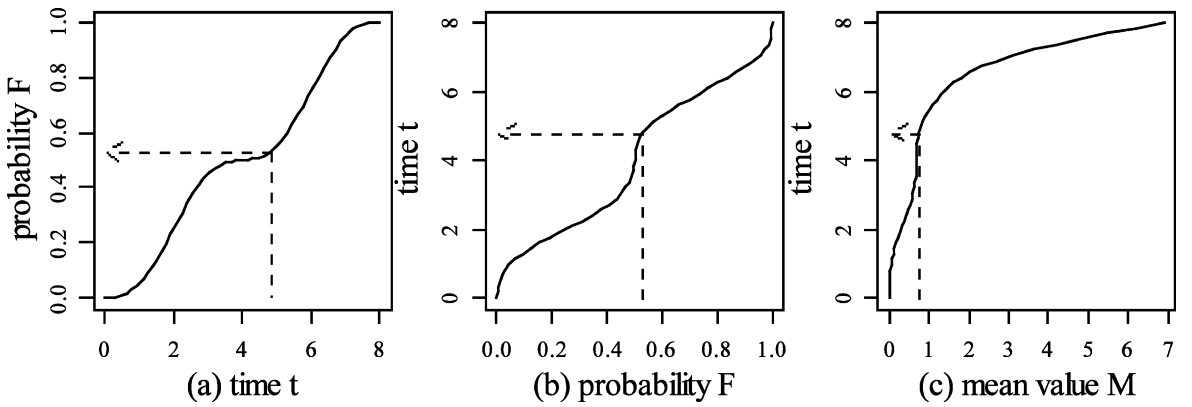

Fig. 4. Time depends on events: (a) usual interpretation of probability F of event by time t; (b) inverse relation with t a function of F; (c) transform from F to mean value M shows how to map time by first randomly picking mean value. Curve is a cubic spline with eight knots.

tions while keeping the decisions simple. The development below shows how this generic biological time can be easily modified to adjust to individual biological clocks. It allows considerable flexibility with environmental effects and interactions among individuals.

For each individual i and possible future event j, there is a mean value function M_{ij} and a random potential times T_{ij} when that future event may be scheduled to occur. We characterize possible modifications to an underlying common mean value function $M_j(t)$ in terms of five non-negative parameters that approximately transform clock time into individual biological time: a = dispersion, b = location, c = intensity, d = truncation and e = rejection (Table 1). $M_j(t)$ is developed using prior experimental knowledge, but the five parameters change during the simulation based on an individual's life history. The future event time is scheduled by sampling V and setting

$$T_{ij} = M_{ij}^{-1}(V) = aM_j^{-1}\left[\frac{G(d) + V}{c}\right] + b$$

unless $V = G(e)$, in which case the event is rejected (censored) and hence never scheduled. Further, events before time $aM_j^{-1}(G(d)/c)+b$ are truncated and never observed. Dispersion a is analogous to Cox (1972) proportional hazards, while intensity c corresponds to accelerated lifetime (Viertl, 1988; Clarotti and Lindley, 1988).

The flexibility of this family of curves is illustrated in Fig. 5, where each parameter except rejection is varied individually. Fig. 6 shows how to achieve a modest reduction or extension in mean time to event by changing each of the five parameters, with markedly different results. These parameters adjust individual biological clocks with useful, intuitive biological interpretations. Disper-

Table 1
Effects of each of the five parameters that transform clock time into biological time based on exponential random variate V

Description	Parameters	Time	Mean value	Range
Identity	[1,0,1,0,1]	$T = M^{-1}(V)$	$V = M(T)$	
Dispersion	[a,0,1,0,1]	$T = aM^{-1}(V)$	$M(T/a)$	$a > 0$
Location	[1,b,1,0,1]	$T = b + M^{-1}(V)$	$M(T-b)$	$b \geq 0$
Intensity	[1,0,c,0,1]	$T = M^{-1}(V/c)$	$cM(T)$	$c > 0$
Truncation	[1,0,1,d,1]	$T = M^{-1}(V + G(d))$	$\max(0, M(T) - G(d))$	$0 = d < 1$
Rejection	[1,0,1,0,e]	$T = M^{-1}(V)$ provided $V < G(e)$	$\min(M(T), G(e))$	$0 < e = 1$

Mean value is expected number of events. Parameters are non-negative, with range constraints indicated.

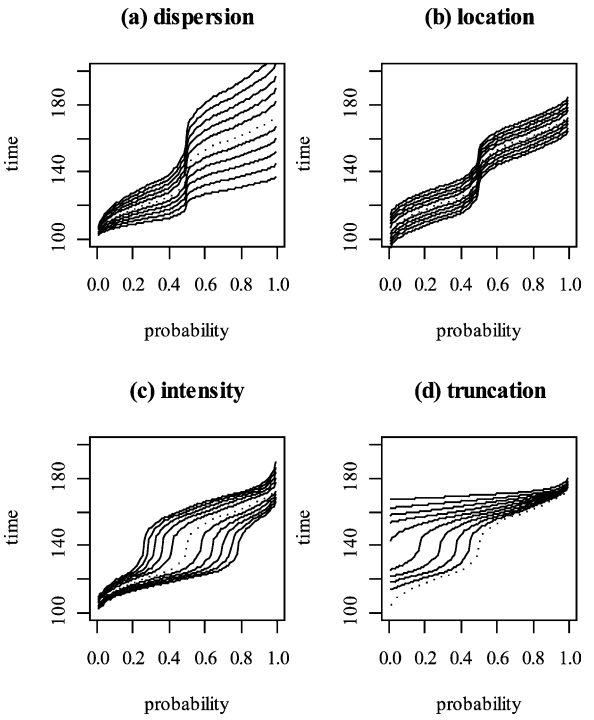

Fig. 5. Four of the five parameters transform the probability to time mapping. Basic curve is from Fig. 1 with dispersion = 10 and location = 100: (a) dispersion varies from 5 to 15; (b) location varies from 90 to 110; (c) intensity varies geometrically from 2.25 to 1/2.25; (d) truncation varies from 0 to 1.

sion can slow or speed the time to the next event. Location is often set to the time of the previous future event, or it can shift probabilities uniformly, postponing events in response to changing conditions. Intensity can raise or lower the mean number of future events, while keeping the same shape M, corresponding to changes in the environment such as reduced food supply.

Truncation and rejection ease simulation of immigration and emigration, respectively. Immigrants can move into an area and continue life processes based on imperfect information. An important future event for such a truncated individual may have happened at some unknown time before it entered the simulation. Emigrants can leave an area with future events unknown and irrelevant. Rejection allows removal of such individuals, eliminating scheduling of their future events. As an example, consider an adult *Aphytis* arriving at an orange to attack red scale. This individual may enter the simulation with very little knowledge of its previous life history except its age, egg load and direction of travel. The *Aphytis* is an immigrant, with a truncated life history. Eventually this invader may oviposit in red scale, laying eggs and ultimately creating a new population of adult *Aphytis* that may either attack nearby red scale or emigrate to another orange tree. Finally, the original flying adult may leave the orange, never to return. While it, and its offspring, may attack other red scale, it is lost to the present simulation. Therefore, at emigration its remaining life history is rejected, as its future is irrelevant.

4.4. Handling immediate events

There are occasions when it may be appropriate to schedule an event without knowing its outcome. At the time of that future event, its specific outcome may be predicted based on the environment and current state of the simulation. Which of the n hosts is attacked by a parasite? The future event is scheduled based on the parasite, but its consequence disrupts a particular host, chosen when the parasitism event occurs as an immediate event. Hosts in the vicinity of the parasite are scored in terms of proximity, size, developmental stage and other factors that may affect the chance of being chosen. The parasite selects a host on which to oviposit with probability proportional to this score. Once a host is selected, there is a further chance mechanism as to whether a male or female egg would be oviposited. Either way, the red scale is immediately rescheduled for death (see Fig. 3).

In some situations, it may be more appropriate to schedule the future event of a prey dying, handling the predators with immediate events. For instance, with a host death at time t, the probability that predator i is the primary beneficiary may be proportional to its mean value function

$$p_i = \frac{M_i(t)}{M(t)}, \quad i = 1, \ldots, n.$$

The immediate event that predator i has the kill is processed with probability p_i. This immediate

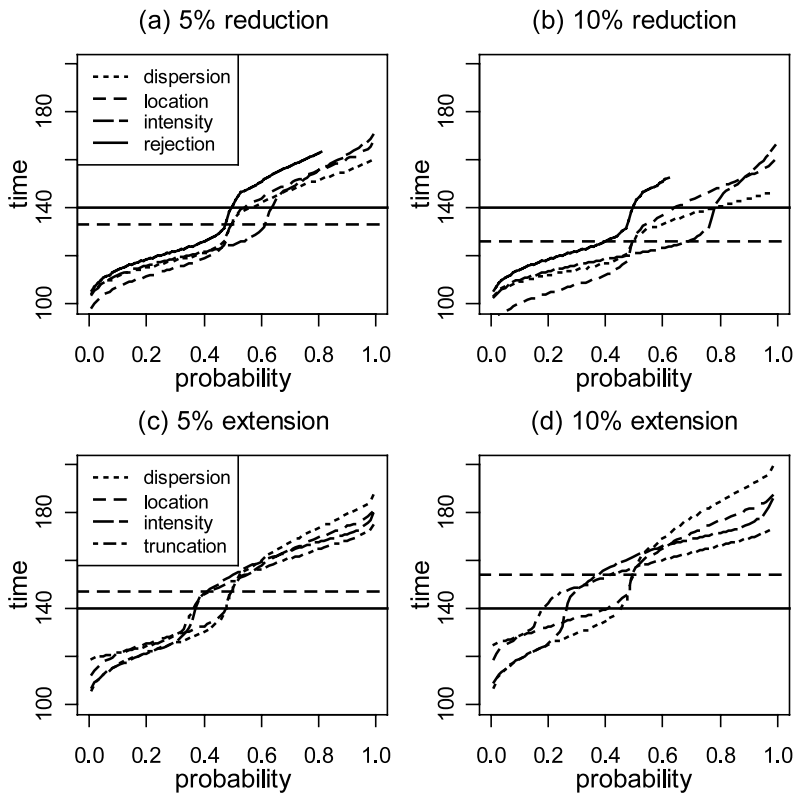

Fig. 6. Modification of five parameters for time reduction or extension: (a) 5% and (b) 10% time reduction via dispersion (dot), location (dash), intensity (long dash) and rejection (solid); (c) 5 and 10% time extension via dispersion (dot), location (dash), intensity (long dash) and truncation (dot dash). Horizontal dashed line is at original mean time; solid line at reduced or extended mean time.

event may cause scheduling of future feeding events for one or more other predators, based on how much the top predator consumes. Once these are scheduled, the process continues as before, but with a newly modified competing risk structure.

An immediate event that spawns multiple future events may need a decision of how many events are to be created. The number of live births may be random, and hence can be drawn from an appropriate distribution, say a histogram based on experimental data suitably modified by environmental considerations (temperature), health of the individual, and actions of other individuals.

5. Simulations

A simulation system has been developed using the event-driven competing risk structure outlined above. The initial implementation focuses on the California red scale–*Aphytis* system, although the software module has no code specific to this system except details of event handling. Our parameterization can dramatically reduce disk storage needs and run time for simulations. Calculations involve no integration, reducing to an exponential random variate, a pair of linear transformations and an evaluation of M^{-1}. The structure of an individual is divided into the "static" properties, such as physical attributes and relationships with other individuals, and the "dynamic" event structure, influenced by the competing risks and other individuals in the community.

Since red scale is temperature-dependent (approximated by degree-days, the integral of degrees above 11 °C) while *Aphytis* is diurnal (active from about 9 a.m. to 4 p.m.), we allow the two species to

operate on different biological clocks. Mean value functions for future events are by default linear in the species-specific biological clock (degree-day or diurnal), but can be tuned using a graphical interface. The software is written in the R language, which is graphical, extensible, and in the public domain (Venables and Ripley, 2000; see http://www.r-project.org). We compute M and M^{-1} and the hour/degree-day translation using forward and backward cubic splines via library (splines) in R, and efficiently generate standard exponential pseudo-random numbers using the R implementation of algorithms by Ahrens and Dieter (1974, 1988). Details of the simulation and access to public domain software can be found at http://www.stat.wisc.edu/~yandell/ewing.

The simulation uses life history information from Forster et al. (1995) as summarized earlier in this paper. A temperature range 15 °C–30 °C is used to represent springtime conditions in the interior regions of California or the San Joaquin Valley. The cool evenings slow development of red scale. We simulate the red scale–*Aphytis* system with varying number of individuals of each species. Here we present a limited set of simulations to demonstrate proof of concept. Initial simulations are run for up to 10,000 events, or several generations of each species.

An isolated population of red scale demonstrates, as expected, an exponential increase in total population over generation (not shown). Since the underlying orange resource is not restricted, we see uncontrolled growth. However, both gravid females and crawlers tend to show inherently discontinuous dynamics, with periods of growth and decline.

A simulation with 200 red scale and 200 *Aphytis*, weighted initially toward immature individuals, shows the characteristic lag in response to parasitization (Fig. 7). The number of red scale initially rises, and then is dramatically reduced by the emerging adult *Aphytis*. Both decline for some time, but the red scale shows evidence of recovery with an increased number of crawlers, and subsequent increase in instars that can serve as *Aphytis* hosts. The decline in *Aphytis* appears to be arrested late in the simulation, but there are only a few individuals left. The frequent vertical spikes in number of *Aphytis* young represent male offspring that are born and immediately removed from the simulation. This crash in parasite population may be due to the artificial isolation of this simulation. In a larger simulation, there could be immigration of new adult *Aphytis* from neighboring orange fruits as well as the emigration of males.

The next example differs in having initial populations of 300 red scale and 50 *Aphytis*, and a slower depletion of adult *Aphytis* egg resources. Fig. 8 shows that *Aphytis* can maintain its population for a few generations. However, as the number of adult *Aphytis* stabilizes at around 35, they begin to seriously reduce the host population. The *Aphytis* population drops as well, as the adults fail to find red scale that are mature enough to support female *Aphytis* eggs. Eventually the remaining *Aphytis* adults would perish for lack of food.

6. Summary and conclusion

This report presents a new and different approach to modeling the structure and dynamics of interacting populations. The philosophy behind the technique has one guiding principle that the biology imbedded in the data collected by the field researcher should drive the model. Both data and model have implicit resolution and span. The keys to this approach are the integrity of data, their relevance to the ecological questions and faithful modeling of their dynamics in the simulation. For example, if the model assumes a random search for prey but the organism displays a very sophisticated search technique, then the model may produce questionable results. In addition, the researcher needs some idea of the various parameters that drive the system such as temperature and possibly humidity for red scale.

We examined the effects of temperature variation on the dynamics of *Aphytis* with respect to red scale. As expected, simulations with many *Aphytis* showed a rapid drop in the red scale population. Further, red scale is rarely driven to "extinction" while *Aphytis* is more likely to disappear, perhaps

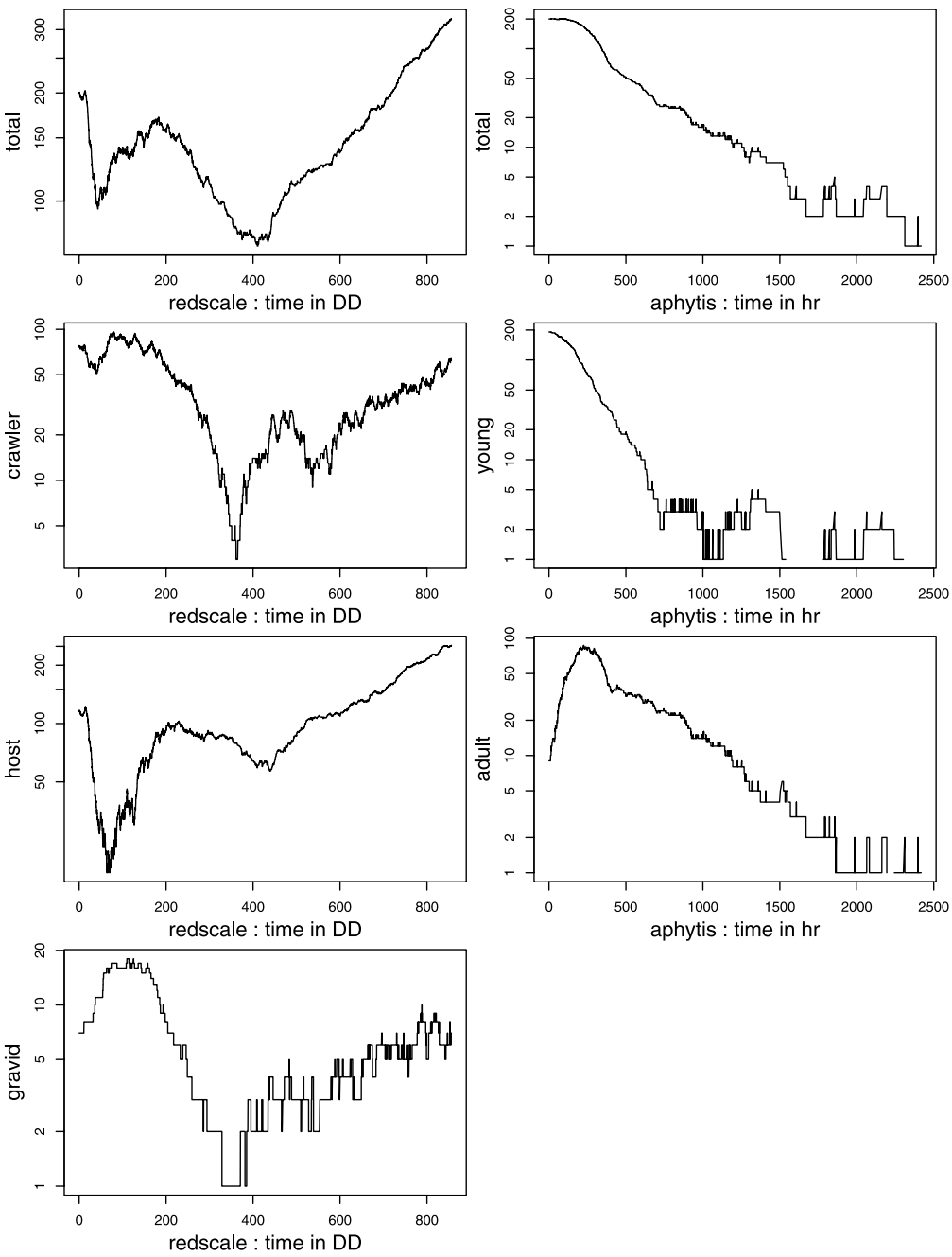

Fig. 7. Red scale and *Aphytis* simulation. Abscissa in units of degree-days and ordinate is log number of individuals with multiple scales by sub-population. Left plots show red scale total (top panel), and summaries for crawlers (crawler), all other stages that can serve as potential parasite hosts (host) and gravid females (gravid). Right plots show *Aphytis* totals (top panel) and summaries by pre-adult stages (young) and the mobile adult stage (adult). Simulation started with 200 red scale and 200 *Aphytis* and ran for 10,000 events, roughly 100 days or 1500 degree-days. This is equivalent to about three generations of red scale and eight generations of *Aphytis*.

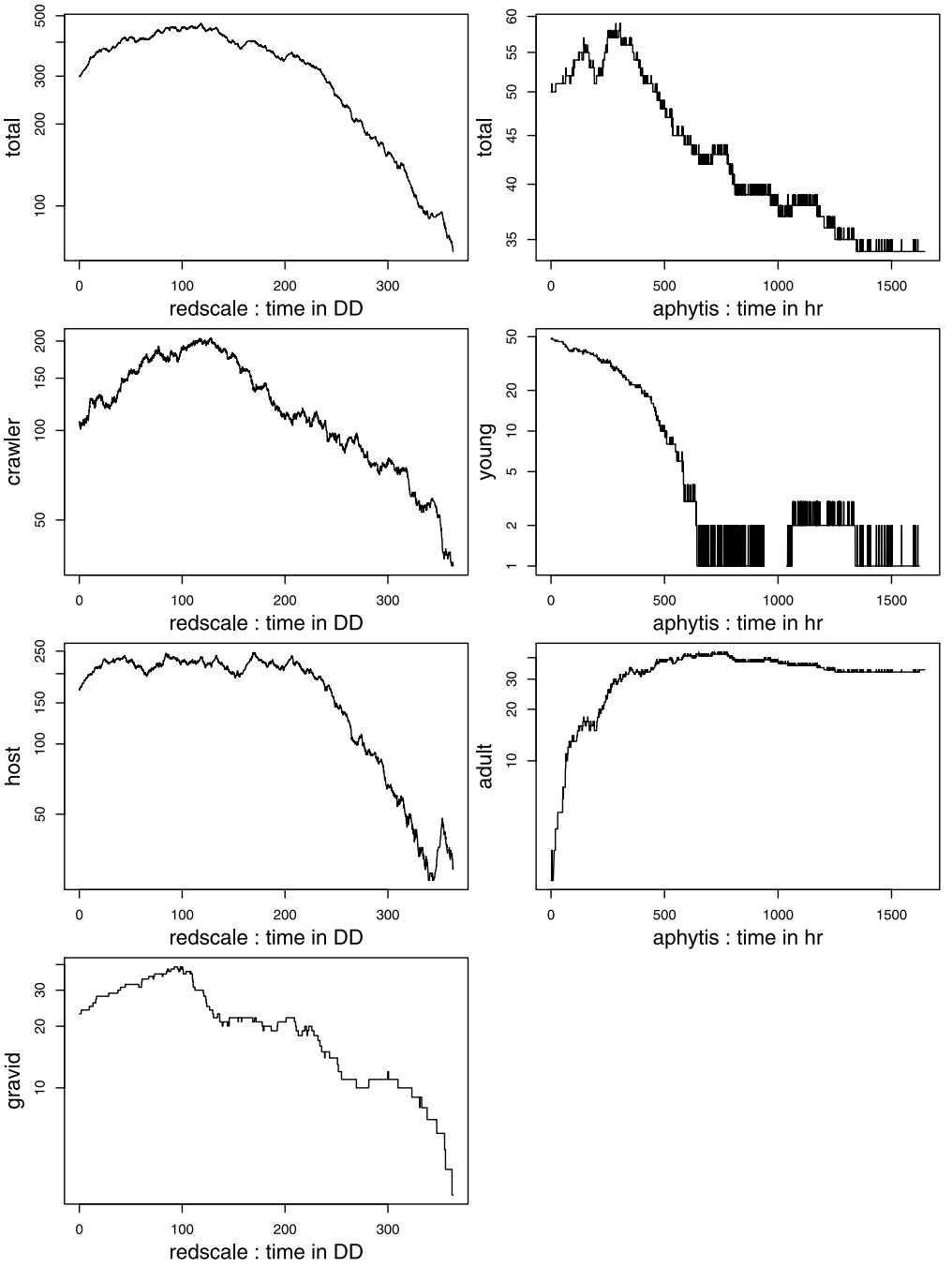

Fig. 8. Simulation started with 300 red scale and 50 *Aphytis* run for 10,000 events, roughly 70 days (six *Aphytis* generations) or 650 degree-days (one red scale generation). *Aphytis* had half the depletion rate of its egg resources in this simulation. See Fig. 7 for description of plot lines.

because *Aphytis* and red scale operate under different constraints. The development of red scale is essentially temperature-dependent, whereas parasitism by *Aphytis* is a time-dependent phenomenon.

The structure of our model system allows easy implementation of modular event algorithms as they become available. We readily admit that the present implementation simplifies the migration pattern for red scale and search strategies for *Aphytis.* We are developing more realistic search and migration algorithms that are fast to compute. In addition to *Aphytis*, other parasites such as *Encarsia perniciosi*, *Comperiella bifasciata* contribute to red scale mortality (Forster et al., 1995). Our simulation system can handle multiple species, and we are investigating these complex interactions.

Analysis of these simulations could proceed using the methods developed for stochastic Petri nets (Ajmone Marsan et al., 1995; Lindemann, 1998; Bobbio et al., 2000), except these methods cannot handle simulations with multiple non-exponential delay times. Instead, we propose to design experiments (Latin hypercubes and response surface methods) by adjusting simulation components and to evaluate the model performance using Bayesian approaches to uncertainty analysis (cf. Kennedy and O'Hagan, 2001 and references therein).

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