



## A dynamic host selection model for mountain pine beetle, *Dendroctonus ponderosae* Hopkins

Alex M. Chubaty<sup>a,\*</sup>, Bernard D. Roitberg<sup>a</sup>, Chao Li<sup>b</sup>

<sup>a</sup> Department Biological Sciences, Simon Fraser University, 8888 University Drive, Burnaby, BC V5A 1S6, Canada

<sup>b</sup> Canadian Forest Service, Northern Forestry Centre, 5320 - 122 Street, Edmonton, AB T6H 3S5, Canada

### ARTICLE INFO

#### Article history:

Received 16 February 2008  
Received in revised form 18 January 2009  
Accepted 31 January 2009  
Available online 9 March 2009

#### Keywords:

Host selection  
Bark beetles  
*Dendroctonus ponderosae*  
Energy reserves  
Dynamic state variable model  
Allee effect

### ABSTRACT

The link between individual habitat selection decisions (i.e., mechanism) and the resulting population distributions of dispersing organisms (i.e., outcome) has been little-studied in behavioural ecology. Here we consider density-dependent habitat (i.e., host) selection for an energy- and time-limited forager: the mountain pine beetle (*Dendroctonus ponderosae* Hopkins). We present a dynamic state variable model of individual beetle host selection behaviour, based on an individual's energy state. Field data are incorporated into model parameterization which allows us to determine the effects of host availability (with respect to host size, quality, and vigour) on individuals' decisions. Beetles choose larger trees with thicker phloem across a larger proportion of the state-space than smaller trees with thinner phloem, but accept lower quality trees more readily at low energy- and time-states. In addition, beetles make habitat selection decisions based on host availability, conspecific attack densities, and beetle distributions within a forest stand. This model provides a framework for the development of a spatial game model to examine the implications of these results for attack dynamics of beetle populations.

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### 1. Introduction

Modeling efforts describing population-level consequences of individuals' habitat use are typically individual-based simulation models (IBMs) (e.g., Fankhauser and Enggist, 2004; Charles et al., 2008). IBMs take a bottom-up approach to elucidate higher-level (i.e. population) patterns, whereas analytical state variable models take a top-down approach (e.g., Logan et al., 1998; Biesinger et al., 2000). While IBMs may provide added realism through the consideration of an individual's state (e.g., physiological), individual behaviour in these models is often represented as probabilities describing the likelihood of the behaviour occurring. On the other hand, analytical state variable models may be used to describe behavioural rules used by individuals, but these behavioural rules tend to describe behavioural averages and thus do not consider individual variation (Grimm, 1999), despite the importance of individual variation in many systems.

Dispersing organisms making habitat selection decisions, evaluate habitat opportunities based on the availability of limited resources in these habitats, the level of competition for these resources, as well as the availability of alternative opportunities

(Muller et al., 1997). Habitat selection theories, such as the ideal free distribution theory (Fretwell and Lucas, 1970), examine the distributions of organisms across habitats (i.e., the outcome of habitat selection behaviour) and are not generally designed to consider the mechanisms underlying these distributions (i.e., habitat selection behaviours themselves, but see Abrahams, 1986). Habitat selection can be considered a general optimal foraging problem: an organism making a decision between two (or more) habitats seeks to maximize the payoff (e.g., energy gains, fitness) relative to the costs of searching or travel (e.g., time, energy losses, missed opportunities). More realistic models of habitat selection necessarily become more complex and impose limitations (e.g., sequential search, time-constraints), which can affect the habitat selection decisions organisms make. Limiting an organism's search opportunities (e.g., short dispersal stage or high dispersal mortality) may result in higher individual fitness when accepting suboptimal habitats if the likelihood of finding optimal habitats is low. Similarly, imposing time-constraints lowers acceptance thresholds for lower quality habitats (Ward, 1987; Stamps et al., 2005). Furthermore, environmental variability and interactions with other individuals require increased behavioural flexibility in making habitat selection decisions because what may be considered optimal under certain sets of conditions may be suboptimal under others (Komers, 1997; Elkin, 2004). Thus, organisms may exhibit flexible host selection behaviour in variable environments in response to these additional constraints.

\* Corresponding author. Tel.: +1 778 782 4512; fax: +1 778 782 3496.  
E-mail address: [achubaty@sfu.ca](mailto:achubaty@sfu.ca) (A.M. Chubaty).

Here we consider how constraints on individuals' habitat search influence behavioural decisions of habitat settlement by examining tactical habitat selection decisions of a time- and energy-limited forager. In such situations, and where mating is contingent upon successful habitat (i.e., host) selection, it is especially important to allow for and consider partial preferences, which may be flexible and change over time. We take into account that an organism's decision to reject a particular habitat at one point in time should not affect the possibility of accepting similar habitat in the future (Ward, 1987). Previous habitat selection models generally have not considered the impact of both time and energy states on individual decisions. These relationships are expected to play an important role in shaping the distributions of individuals in time and space, and thus, may have significant implications for species conservation and pest management.

The mountain pine beetle, *Dendroctonus ponderosae* Hopkins (Coleoptera: Curculionidae: Scolytinae) (MPB), is an aggressive bark beetle species native to pine forests of North America, which primarily attacks lodgepole pine (*Pinus contorta* Dougl. ex Loud var. *latifolia* Engelm.) (Rudinsky, 1962; Wood, 1982; Safranyik and Carroll, 2006). Reproduction in bark beetles is contingent upon successful search for and attack of a suitable host tree, which, unlike other phytophagous insects, results in tree death. Host search involves both visual and olfactory cues, including beetle-produced pheromones involved in coordinated 'mass attack' required to overcome host defences including toxic secondary compounds and resin secretions (Atkins, 1966a; Wood, 1982; Raffa and Berryman, 1983; Berryman et al., 1985). The extent of these defences varies between individual trees, and they may only be overcome if a sufficiently high number of beetles attack an individual tree over a short period of time, thereby exhausting the defensive capabilities of the tree (Raffa and Berryman, 1983). At low attack densities, individual beetles face almost-certain death, especially against vigorous trees, and thus benefit from conspecifics joining the aggregation (i.e., an Allee effect, Allee, 1931). However, at very high beetle attack densities, larval competition for resources (phloem) increases substantially and can have significant deleterious effects on overall brood production (Reid, 1963; Raffa and Berryman, 1983; Safranyik and Carroll, 2006).

Individual beetles must therefore search for a host which will yield the greatest amount of resources for use toward reproduction relative to the individual risk and effort to overcome host defences. As alluded to above, beetles are choosy and discriminate among hosts based on size, quality, and defensive capability, as well as conspecific (attack) densities; and evaluate them based on gustatory cues (Raffa and Berryman, 1982). Beetles favour large diameter trees and those with thick phloem, as phloem thickness is positively correlated with brood production (Reid, 1963; Berryman, 1976; Safranyik and Carroll, 2006). However at low beetle population densities they will attack weakened or stressed trees (Rudinsky, 1962; Safranyik and Carroll, 2006).

The extent of this 'choosiness' is likely modulated by individual energy reserves (Atkins, 1966b). Bark beetles use lipids to power flight and beetles generally do not feed after emerging from their natal trees (Atkins, 1969; Wood, 1972; Elkin and Reid, 2005). Thus, they are limited in the duration and extent of their host-search period. Furthermore, beetles become more receptive to hosts after a minimum flight period (Shepherd, 1966; Safranyik and Carroll, 2006), suggesting that host acceptance is dependent on the energy state (i.e., lipid reserves) of the beetle. We take this energy state-dependent approach to explain what a bark beetle should do when it encounters a host tree.

Using a theoretical modeling approach, we examine beetles' 'choosiness' as a complex interaction between the energy state of the individuals, and their environment (i.e., the trees available in a forest stand, as well as the number of other individuals). We

develop a dynamic state variable (DSV) model, which is ideally suited for examining this behaviour at the individual level, and can be readily expanded upon to consider population-level processes and effects such as population and attack dynamics. Major impacts of MPB infestation include the effects on forest community dynamics, the economic impact on timber supplies, and the effects on climate change (Kurz et al., 2008). These impacts warrant explicit examination of how individual behaviour may shape population processes, thus, we construct a DSV model of individual MPB host selection, based on an individual's energy state, as a necessary first step toward the development of a strategic state-dependent model of host selection.

To assist with parameterization of the model presented here, we collected data to assess the availability and distributions of potential host trees in a forest stand representative of suitable MPB habitat.

## 2. Methods

### 2.1. Model description

#### 2.1.1. Dynamic state variable (DSV) models

DSV models are optimization models that have been used for a variety of applications, including behavioural ecology, where they have been employed to solve such problems as patch and host selection and oviposition decisions in parasitoids (Li et al., 1993; Wajnberg et al., 2006; Roitberg and Bernhard, 2007). Unlike other types of models, DSVs explicitly consider one or more dynamic states. In general, DSV models calculate the expected fitness payoff associated with each of a possible set of outcomes (i.e., decisions), and select optimal decisions that maximize fitness. (*Note:* 'decision' in this case does not mean a conscious decision on the part of the organism.) Specifically, these optimal decisions are solved numerically using the process of 'backward iteration': fitness values at the end of time are computed first, and then working backwards through time, the remainder of the values are computed (Bellman, 1957; Mangel and Clark, 1988; Clark and Mangel, 2000). Furthermore, our choice of an economic model subsumes underlying genetic variation in habitat selection behaviour without specifying exact mechanisms (Grafen, 1984).

#### 2.1.2. MPB-DSV model

Female mountain pine beetles take flight in late summer in search of suitable hosts in which to lay their eggs. They rely on lipid stores to power their flight and are not known to feed once leaving their natal tree. In addition, beetles have a limited amount of time to find a suitable host, begin gallery excavation, and lay their eggs, since their larvae must develop past the second instar stage to overwinter (Safranyik and Carroll, 2006). Given these constraints, this model considers two state variables, energy ( $x$ ) and time ( $t$ ), where fitness ( $F$ ) is accrued only if a host is found and accepted before terminal time ( $T$ ), and a beetle's energy state is greater than zero. We define fitness at terminal time as  $F(x, T) = \Phi(x)$ , where  $\Phi(x)$  is the terminal fitness function representing total future reproduction (A.1), and where  $x_{\min}$  is the minimum energy level below which successful reproduction is not possible, yielding the equation

$$\Phi(x) \begin{cases} = 0 & \text{if } x \leq x_{\min} \\ \in (0, 1] & \text{if } x_{\min} < x \leq x_{\max}. \end{cases} \quad (1)$$

The model maximizes fitness over two behavioural decisions: the first is whether to stay in or leave the current (i.e., natal) stand, and the second is whether to accept or reject a particular new host with a certain density of beetles if it is encountered. There is no opportunity to return to the natal stand once the decision to leave is made, and a beetle cannot leave a host once a decision to accept that

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