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On-Bark Behavior of *Dendroctonus frontalis*: A Markov Chain Analysis

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Tree-killing species of the Scolytidae (Coleoptera) must locate suitable hosts at least once per generation for successful reproduction. The process used to select hosts is complex, involving a sequence of steps and many possible outcomes. Because more beetles land on bark (host-find) than bore galleries (host-recognize), postlanding behaviors appear to be important in determining whether a potential host is selected. We applied Markov chain analysis to on-bark behaviors of the southern pine beetle, Dendroctonus frontalis *Zimmermann, that were described by previous investigators. Predictions obtained from our analysis agree well with earlier descriptions and provide additional information not heretofore apparent. By developing chains for each sex, sexually dichotomous fighting behaviors were revealed. Testable predictions were generated for outcomes of complex interactions that occurred when tree resistance and predator density were varied. Markov chain analysis also provides a framework for future host selection studies. Use of this type of analysis requires collecting data over the entire behavioral sequence of interest, with concentration on estimating the transition probabilities among states. This approach provides results for the many possible outcomes derived from a sequence of interrelated activities. We expect that such an integrated*

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treatment will lead to a greater understanding of important facets of scolytid host selection behavior.

KEY WORDS: Scolytidae; southern pine beetle; host selection; host recognition; transition probabilities; absorbing states.

INTRODUCTION

Adult bark beetles (Coleoptera: Scolytidae) require suitable host trees to attract mates, deposit eggs, and survive. This makes host selection a critically important phase in the life cycle of bark beetles. Host selection is a complex process that may be described by five steps: host-habitat finding, host finding, host recognition, host acceptance, and host suitability (Kogan, 1994). The process is catenary in that the steps must be completed in sequence to achieve a successful end. In analysis of pine bark beetle behavior, host finding has received the most attention because of its interrelationship with semiochemicals used in mass attack. For the southern pine beetle, *Dendroctonusfrontulis* Zimmermann (Coleoptera: Scolytidae), host finding is aided by a suite of pheromones and host compounds that both attract and dissuade beetle landing (Payne, 1980). Pest managers have taken advantage of these chemically mediated behaviors by applying attractants and antiaggregants to monitor populations and disrupt infestations of *D. frontalis (e.g.,* Clarke *et al.,* 1999).

In contrast to host finding, cues used in host recognition and host acceptance are incompletely understood, leaving no behavior-based targets for disruption connected with these steps. Studies suggest that host recognition by scolytids generally requires gustatory stimulation from the bark (Elkinton and Wood, 1980) and that host chemicals play a role in biting (Hynum and Berryman, 1980; Thomas *et al.,* 1981; Raffa and Berryman, 1982) plus tunneling (e.g., Wallin and Raffa, 2000) behaviors. Both host recognition and host acceptance occur after arrival on a potential host tree. Because many more beetles land on bark (host-find) than bore galleries (host-recognize), postlanding behaviors appear to be important in determining process results. Greater understanding of on-bark behavior will provide important information about the process of host recognition and may aid in its disruption by pest managers.

Research on host recognition and acceptance commonly proceeds by manipulating an individual cue for a targeted modality (e.g., the effects of a particular chemical on olfaction or gustation). While this approach may be informative, it does not lend itself to evaluating or quantifying the potential effects of treatments on the outcome of the process of interest. For example, particular host chemicals have been shown to reduce the number of individuals caught (e.g., Hayes *et al.*, 1994), to increase mortality (e.g., Coyne and Lott, 1976), and to retard gallery construction (e.g., Wallin and Raffa, 2000) of targeted scolytids. However, traditional approaches are not sufficient for evaluating effects of host chemicals on the complex and polychotomous process of host selection. It may be that compensatory or redundant behaviors lead to different kinds of effects when the overall process of host selection is considered. Plasticity in behavior of scolytids during host selection is likely important given that beetles encounter a range of concentrations in host chemicals both within and among host species (Mirov, 1961; Smith, 1977; Hodges *et al.*, 1979). This could help explain the significant difficulties encountered in manipulating insect herbivores when using deterrents known to have significant behavioral effects (e.g., Foster and Harris, 1997; Strom *et al.*, 2004).

Development of quantitative techniques that are appropriate for evaluating serial processes with multiple outcomes, such as those found in insect host selection, promises to increase the amount and utility of information gained over that provided by single-stimulus studies. Coupling these methods with observations made in *situ* allows the assessment of transitional probabilities among behaviors, and the estimation of their ultimate impact on process outcomes. This leads to more fundamental questions about such outcomes rather than about particular behavioral events. Markov chains (Kemeny and Snell, 1960; Taylor and Karlin, 1998) are particularly suited for investigation of connected sequential observations and can provide important information not immediately apparent from observed frequencies. Their use in biology often focuses on movement of individuals from one category to another, for example, between life stages or physical locations. Weissburg *et al.* (1991) used Markov chains to model hermit crab occupancy of gastropod shells. Similarly, Huelsenbeck *et al.* (2000) employed Markov chains to analyze host switching of parasites, while Woolhouse and Harmsen (1989) modeled changes in abundance of European red mites in an apple orchard via chains.

In this paper, we use Markov chain analysis to reanalyze on-bark observations reported by Bunt *et al.* (1980) for *D. frontalis*. Those investigators grouped postlanding activities into categories and focused on the sequential nature of these behaviors. They reported relative frequencies of beetle movements from one category to another, as well as frequencies of termination activities, such as dropping off a tree or being eaten by a predator (Fig. 1). Markov chain analysis increases the behavioral information obtained from these data and allows a more complete understanding of the processes involved in host recognition and acceptance, while also providing a framework for additional research.

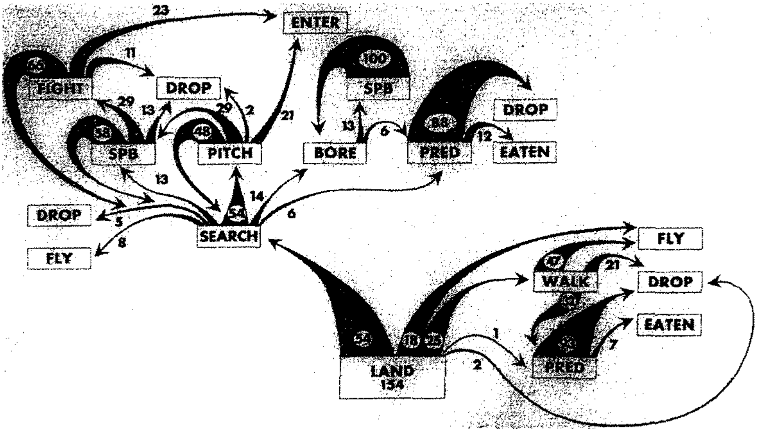

Fig. 1. On-bark behavioral sequence of the southern pine beetle presented by Bunt *et al.* (1980). Numbers represent observed percentages of beetles that moved to categories indicated by the arrows (n = 154). (Reproduced by permission of the Entomological Society of America.)

BACKGROUND INFORMATION

The study by Bunt *et* al. (1980) serves as the basis for this investigation and provides the observations. This research was conducted in an active *D. frontalis* infestation in an uneven-aged pine-hardwood forest in East Texas during 1978. Beetle postlanding behavior was observed on a 0.28-m’ (70 x 40-cm) region of the bole of each of six beetle-infested loblolly pines (*Pinus taeda* L.). Between 22 and 29 beetles landed within each of the six bark areas during four days of observation (154 beetles total). In addition to observations of behavior within the study regions, beetles were caught in landing traps located just above each area for determination of sex ratio. Beetles that entered the trees at points within the bark study areas also *were* later counted and sexed.

Beetle activities within the six study regions were separated into two classes: on-bark activities and termination behaviors. The former included landing (LAND), walking (WALK), searching (SEARCH), investigating an entrance hole (PITCH), boring into the bark (BORE), encountering another southern pine beetle (SPB), encountering a predator (PRED), and fighting with another southern pine beetle (FIGHT). Termination behaviors included flying from the tree (FLY), dropping off the tree (DROP), being captured by a predator (EATEN), and entering an existing hole (ENTER). For these observations, no distinction was made between sexes.

Of the 154 beetles that landed in the study areas, 126 were followed until either successful entrance into the host tree or departure from the tree. The other 28 beetles were lost, mostly in bark crevices. Transitions among on-bark behaviors were recorded for all observed beetles (e.g., of the 154 that landed, 54% initiated searching activity, 25% began walking with no apparent goal, 2% dropped off the tree, 1% encountered predators, and 18% immediately flew away). Figure 1, which summarizes the sequential activity patterns of on-bark beetles, exhibits all transition frequencies observed by Bunt *et al.* (1980). These data form the starting point of our analyses.

In addition to transition frequencies, the authors reported frequencies of termination behaviors for the 126 individuals observed throughout their stay (for instance, 54 of the 126 flew from the tree, while 42 dropped off). These data are compared below with predictions obtained from analysis of transition data, as a partial check on our methods (Table VI).

MARKOV CHAIN DESCRIPTION

In the language of Markov chains, activities are called "states," on-bark activities being "transient," while termination activities are "absorbing" (Kemeny and Snell, 1960; Taylor and Karlin, 1998). A beetle currently in a transient state can move to other states but eventually will enter an absorbing state. In Markov chains, an absorbing state, once entered, is never left. EATEN is clearly such a state, but in our chain so is ENTER, because a beetle that enters an existing hole moves beyond the scope of observation. In this sense our Markov chain models only the on-bark portion of the host selection process.

For purposes of analysis, all information about a Markov chain is contained in its "transition probabilities," numbers that represent probabilities of moving, in a single "step" or "transition," from each state to every other state. For example, Fig. 1 indicates that of all observed beetles engaged in walking behavior, 21% then dropped off the tree, 47% flew away, and 32% encountered a predator. Thus, in the chain, a beetle in state WALK is assigned respective probabilities 0.21, 0.47, and 0.32 of moving in one step to states DROP, FLY, and PRED and zero probability of moving to any other state.

Three adjustments to Fig. 1 are needed to meet requirements for Markov chain analysis. First, a central assumption in Markov theory is that transition probabilities from a state remain the same regardless of when the state is entered or which particular states were visited previously. While acceptance behaviors of some beetle species can change with altered stimuli such as physiological state and presence of conspecifics (Wallin and

Raffa, 2000, 2002), as reported below, predictions based on the above assumption agree well with the termination data recorded by Bunt ***et al.*** (1980).

In Fig. 1, a beetle can encounter other beetles (SPB) either during search activity or while attempting to bore into the bark. Subsequent behavior differs, however, depending on which type of encounter occurs. An encounter while boring always leads to continuation of boring, while an encounter during searching is followed by dropping off the tree, fighting, or a return to searching. In keeping with the above assumption, we use SPB to represent the second of these types of encounter and treat observed encounters with other southern pine beetles during boring as though no encounter took place.

Second, a beetle can encounter a predator (PRED) immediately after landing, while walking (WALK) or while searching (SEARCH). In Fig. 1, frequencies of dropping from the tree (DROP) or being predated (EATEN) differ depending on when the encounter occurred. To meet chain requirements, we assume that these differences can be attributed to sampling variation and use the "average" transition probabilities listed in row PRED in Table I.

Third, in addition to possibly encountering a predator or a conspecific, a beetle engaged in boring activity (BORE) can successfully penetrate the tree (PEN) or drown in the resulting resin flow (DROWN), activities not included in Fig. 1. To complete specification of the chain, we add these activities to form Fig. 2. With these modifications, our Markov chain has eight transient states-LAND, SEARCH, WALK, PRED, SPB, FIGHT, PITCH, and BORE-and six terminal, absorbing states-FLY, DROP, EATEN, ENTER, DROWN, and PEN.

Table I is the "transition matrix" (Kemeny and Snell, 1960; Taylor and Karlin, 1998) for the Markov chain associated with Figure 2. Entries represent probabilities of movingfrom states listed at the left in the table *to* states listed at the top. For example, a newly landed beetle has probability 0.18 of flying away without engaging in other activity, probability 0.02 of dropping off the tree, probability 0.54 of initiating search activity, etc.

MALE VERSUS FEMALE CHAINS

Additional assumptions are needed to obtain separate transition matrices for female and male beetles from the Bunt et *al.* (1980) data. Two of these reflect beetle behavior (Payne, 1980): we assume that only females bore into a tree, and only males enter existing holes. As a consequence, BORE and PEN are activities restricted to females, while ENTER is a male-only activity. Because males typically join females and thus do not commonly initiate

Table I. Transition Matrix for the Beetle Population as a Whole, Showing Transition Probabilities Between the Eight On-Bark Activities (Transient States) and the Six Termination Behaviors (Absorbing States) as Described in the Text: Entries Represent Probabilities of Moving from States Listed at the Left of the Array to States Listed at the Top (Empty Cell Entries Are All Zero)

	FLY	DROP	EATEN	DROWN	PEN	ENTER	LAND	SEARCH	WALK	PRED	SPB	FIGHT	PITCH	BORE
FLY	1													
DROP		1												
EATEN			1											
DROWN				1										
PEN					1									
ENTER						1								
LAND	**0.18**	0.02						0.54	0.25	0.01				
SEARCH	0.08	0.05								0.06	0.13		0.54	0.14
WALK	0.47	0.21								0.32				
PRED		0.9	0.1											
SPB		0.13						0.58				0.29		
FIGHT		0.11				0.23		0.66						
PITCH		0.02				0.21		0.48			0.29			
BORE				0.05	0.89					0.06				

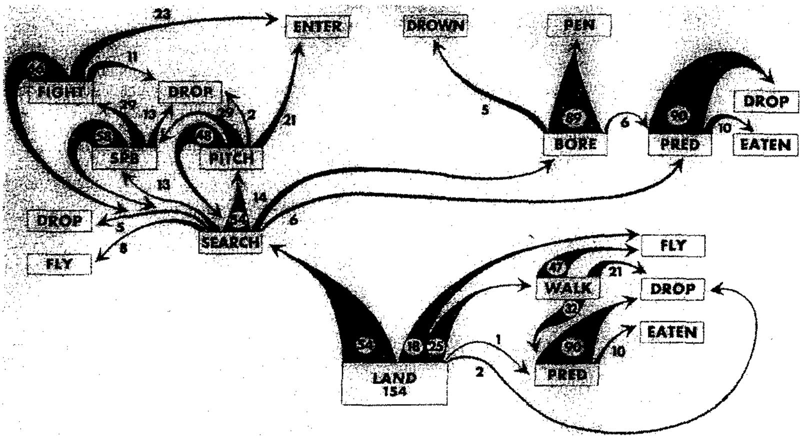

Fig. 2. On-bark behavioral sequence of the southern pine beetle as modified for Markov chain analysis. Figure 1 was altered to fulfill assumptions of Markov chains and to include two additional behaviors. DROWN and PEN.

galleries themselves, we assume that males do not DROWN. This means that females engage in all eight transient activities (LAND, SEARCH, WALK, PRED, SPB, FIGHT, PITCH, BORE) but in only five terminal states (FLY, DROP, EATEN, DROWN, PEN) because they do not participate in the ENTER activity. Males, on the other hand, have seven transient states (LAND, SEARCH, WALK, PRED, SPB, FIGHT, and PITCH) and four terminal states (FLY, DROP, EATEN, and ENTER). Appendix A lists all assumptions used; the respective transition matrices for females and males appear in Tables II and III.

MARKOVIAN ANALYSIS OF ON-BARK BEHAVIOR

Once a transition matrix is specified, standard techniques of Markov chain analysis produce results concerning a beetle's transient behavior and its probabilities of entering the various termination states (Kemeny and Snell, 1960; Taylor and Karlin, 1998).

For the entire mixed-sex population observed by Bunt et al. (1980), entries in the first row in Table IV estimate the average numbers of times a newly landed beetle will engage in the transient behaviors listed at the top of the table, before terminating its onbark activity. For instance, an arriving beetle will initiate searching behavior an average of 1.039 times, encounter another southern pine beetle 0.298 times on average, investigate an existing

Table II. Transition Matrix for the Female Portion of the Beetle Population, Showing Transition Probabilities Between Eight On-Bark Activities (Transient States) and Five Termination Behaviors (Absorbing States) as Described in the Text: Entries Represent Probabilities of Moving from States Listed at the Left of the Array to States Listed at the Top (Empty Cell Entries Are All Zero)

	FLY	DROP	EATEN	DROWN	PEN	LAND	SEARCH	WALK	PRED	SPB	FIGHT	PITCH	BORE
FLY	1												
DROP		1											
EATEN													
DROWN				1									
PEN					1								
LAND	0.18	0.02					0.54	0.25	0.01				
SEARCH	0.08	0.05							0.06	0.13		0.39	0.29
WALK	0.47	0.21							0.32				
PRED		0.9	0.1										
SPB		0.13					0.8				0.07		
FIGHT		0.11					0.89						
PITCH		0.02					0.69			0.29			
BORE				0.05	0.89				0.06				

Table III. Transition Matrix for the Male Portion of the Beetle Population, Showing Transition Probabilities Between Seven On-Bark Activities (Transient States) and Four Termination Behaviors (Absorbing States) as Described in the Text: Entries Represent Probabilities of Moving from States Listed at the Left of the Array to States Listed at the Top (Empty Cell Entries Are All Zero)

	FLY	DROP	EATEN	ENTER	LAND	SEARCH	WALK	PRED	SPB	FIGHT	PITCH
FLY	1										
DROP		1									
EATEN			1								
ENTER				1							
LAND	0.18	0.02				0.54	0.25	0.01			
SEARCH	0.08	0.05						0.06	0.13		0.68
WALK	0.47	0.21						0.32			
PRED		0.9	0.1								
SPB		0.13				0.43				0.44	
FIGHT		0.11		0.26		0.63					
PITCH		0.02		0.32		0.37			0.29		

Table IV. Estimated Average Numbers of Times a Newly Landed Beetle Will Engage in Various Transient Behaviors, for Three Population Categories: The Last Entry in Each Row Is the Sum of the Preceding Entries and Represents the Average Total Number of Behavioral Transitions a Newly Landed Beetle Makes to Reach a Terminal State

Population	LAND	SEARCH	WALK	PRED	SPB	FIGHT	PITCH	BORE	Sum
Total	1	1.039	0.25	0.161	0.298	0.086	0.561	0.145	3.541
Females	1	1.036	0.25	0.17	0.252	0.018	0.404	0.3	3.43
Males	1	1.044	0.25	0.153	0.342	0.15	0.71	0	3.65

hole 0.561 times, etc. The average total number of behavior transitions is 3.54, the sum of the entries in the first row in Table IV Corresponding values for females and males appear separately in the other two rows.

Each row in Table V contains probabilities that a beetle currently engaged in a selected transient activity will enter various termination states. To illustrate, 38% of all newly arrived females will fly away, 32% will drop off the tree, 1.7% will be predated, etc. Entries in each row sum to 1.0 because beetles must terminate ***somewhere.***

After females penetrate a tree, males arrive and search for penetration holes. Males enter holes occupied by unaccompanied females to begin the mating process (Payne, 1980). Thus, the number of males that enter a hole (ENTER) corresponds to the number of females that successfully bore into a tree (PEN). As a check on results obtained from the chain analysis, Table V indicates that 26.7% of females will successfully penetrate a tree on which they land, while 26.6% of newly arrived males will enter a tree.

Table V. Probabilities That Beetles in Selected Categories Will Terminate Their Stay by Entering One of the Absorbing Behaviors Shown at the Top of the Table: Because All Beetles Terminate Somewhere, Entries in Each Row Sum to 1.0

	FLY	DROP	EATEN	DROWN	PEN	ENTER
LAND						
T	0.381	0.329	0.016	0.007	0.129	0.138
F	0.38	0.32	0.017	0.015	0.267	0
M	0.381	0.337	0.015	0	0	0.266
SEARCH						
F	0.153	0.309	0.015	0.028	0.495	0
M	0.155	0.34	0.012	0	0	0.493
FIGHT						
F	0.137	0.385	0.013	0.025	0.441	0
M	0.097	0.324	0.007	0	0	0.571

Note. T, Total Population; F, female; M, male.

Table VI. Terminal Behavior Frequencies Reported for the Total Population by Bunt et al. (1980) Versus Those Predicted by Markov Chain Analysis (see Table V)

	Behavior			
	FLY	DROP	EATEN	ENTER
Observed	0.429	0.333	0.016	0.103
Predicted	0.381	0.329	0.016	0.138

To assess further the validity of the Markov chain approach, we checked predictions generated from our transition matrices against statistics on terminal behavior reported in Table III of Bunt et al. (1980). Although the data in this table relate to the same beetles that produced the frequency data upon which our chain matrices are based, these data sets are otherwise independent. In particular, no data from Table III of Bunt et *al. (1980)* were used to generate our chains. While there are discrepancies between our predicted and their observed values, the termination probabilities obtained from chain analysis are reasonably consistent with observed frequencies (Table VI). Some of the differences may arise because the transition matrix for the chain is based on rates obtained from observations on all 154 beetles, while termination frequencies relate only to the 126 beetles that were followed until reaching a final state.

To compare our predictions with the Bunt *et* al. (1980) data on females and males separately, we used reported numbers of beetles per day that landed in the study regions, together with daily sex ratios found in the landing traps, to arrive at an overall female: male sex ratio of 48.3:51.7. From this ratio, we estimate that 61 females and 65 males were followed throughout their stay in the study areas. Of these, 15 females (12% of 126 beetles observed) successfully bored into the host, while 13 males (10% of 126) found and entered bored holes. Entries in the second and third rows in Table V give corresponding predictions of 61 x 0.267 = 16.3 females and 65 x 0.266 = 17.3 males.

As noted previously, male and female beetles differ in their possible behavioral states. Other behavioral distinctions are also evident from our analysis. Mean numbers of transitions for males and females, following transient states common to the two sexes, are shown in Table VII. Since all on-bark activities begin with landing, values given for the LAND category reflect average total numbers of changes that occur while beetles are on trees. Males tend to experience slightly more behavioral changes than females, both overall and following SEARCH behavior. Females, on the other hand, undergo more transitions than males following FIGHT and PITCH activities,

Table VII. Mean Number of On-Bark Behavioral Changes for Male and Female Beetles Following Each of Seven Transient Behaviors

	Behavior						
	LAND	SEARCH	WALK	PRED	SPB	FIGHT	PITCH
Female	3.43	3.87	1.32	1.0	4.401	4.445	4.949
Male	3.65	4.277	1.32	1.0	4.465	3.694	3.877

primarily because they are more likely to return to searching (see Tables II and III).

Additional information about behavioral choices can be obtained from the male and female chains. Suppose, for example, that a beetle encounters another beetle of the same sex. Its options then are to fight, to drop off the tree, or to resume searching behavior (Tables II and III). Presumably, the ultimate goal of a male beetle is to enter the tree to join a female, while a female seeks to successfully penetrate the bark and construct a gallery. The fifth and seventh lines in Table V predict that, on average, a male that chooses to fight gains more than one that does not, since a fighter has probability 0.571 of eventually entering the tree, while this probability drops to 0.493 if he resumes searching. Corresponding values for female penetration (lines 4 and 6 in Table V) are 0.441 if fighting and 0.495 if searching. These values indicate that a female beetle should avoid fighting and resume searching. Our calculations thus suggest that fighting should be more prevalent among male beetles than among females. The accuracy of this prediction is unknown because on-bark fighting by *D. frontalis* has not been sufficiently investigated.

SENSITIVITY TO VARYING OLEORESIN FLOW AND PREDATOR DENSITY

Markov chain analysis also provides a method for investigating complex interactions among variables that potentially alter beetle behavior. For example, host resistance (as oleoresin yield) and natural enemy density (especially that of *Thanasimus dubius*) may affect population dynamics and host selection behavior of *D. frontalis* (Coulson, 1979; Turchin *et al.*, 1999; Strom *et* al., 2002). As such, they are potential targets for extrinsic manipulation. For example, improving flow of oleoresin at beetle attack sites, which likely impacts successful host finding and recognition (Strom *et al.*, 2002), can be accomplished through silvicultural methods (e.g., tree breeding), while density of clerid predators can be increased through rearing and augmentative release programs. Efficient development of these approaches requires the ability to predict potential outcomes of various deployment strategies. Markov chain analysis provides a method for making such predictions.

Based on studies of resin flow rate in young loblolly stands (Roberds et *al.*, 2004) and mature stands (Cook and Hain, 1986, 1987), Bishir et ***al.*** (unpublished) model the probability of successful penetration by females attempting to bore into a tree as

$$P = 0.94 * 17451/[17,450 + \exp(0.287 * \mathrm{FR})]$$

where FR = resin flow rate [(ml/hr) x 100] and exp denotes the exponential function. FR = 25 is the average rate reported in mature trees (Cook and Hain, 1986, 1987). If, in the last row (BORE) in Table II, we replace 0.89 with P and 0.05 with $0.94 - P$, we can use Markov chain analysis to investigate the sensitivity to changes in resin flow rate, FR, of the probability of eventual host penetration by newly landed *D. frontalis* females. We consider changes that occur as resin flow rates range from FR = 0 to FR = 50.

Similarly, taking the predator density observed by Bunt ***et al.*** (1980) as our standard for relative density ($D = 1$), we can assess effects on landed female penetration and mortality rates as relative predator density is doubled ($D = 2$), quadrupled ($D = 4$), etc. Appendix B describes the process by which we adjust the female transition matrix to reflect changes in predator density.

Figure 3A profiles the changes in penetration probability when FR and D are varied simultaneously. Irrespective of predator density, changes in flow rate alone produce little effect unless FR values are slightly above average (between about 25 and 40). If, on the other hand, FR values are held constant, response to change in predator density is fairly uniform; densities of the order of 10 times the level observed by Bunt ***et al.*** (1980) are required before there is substantial reduction in the probability of beetle penetration.

Changes in on-bark mortality rate (the probability that newly landed female beetles eventually are predated or drowned in resin) follow a more complex pattern (Fig. 3B). As expected, increases in resin flow lead to increased mortality regardless of predator density, although death rate accretion is much reduced at the higher predator densities. Variations in predator density, however, produce unexpected responses. At FR values of 25 and below, overall mortality increases as predator density increases. Surprisingly, the reverse is true at high flow rates: here, increasing predator density leads to ***decreased*** overall mortality. Examination of Fig. 2 helps explain this result. Higher predator densities lead to more beetles dropping from a tree, thus avoiding the elevated rates of drowning in massive resin flow. Such

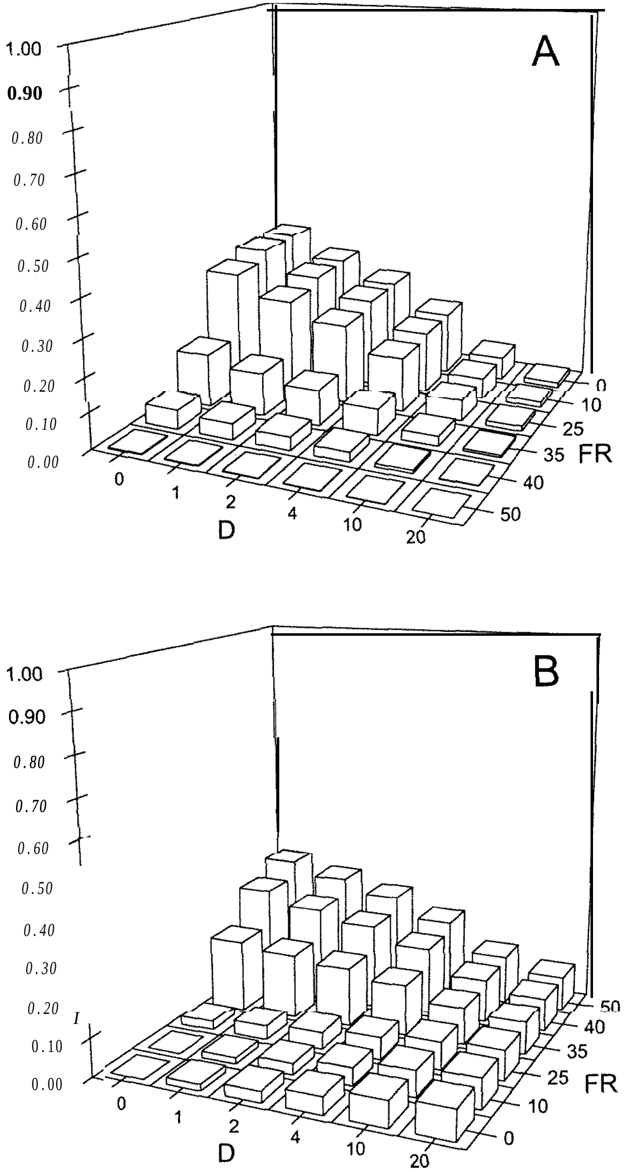

Fig. 3. Effects on (A) the probability of eventual bark penetration by newly landed female southern pine beetles and (B) the probability of on-bark mortality of newly landed female southern pine beetles that resulted from changes in predator density D and oleoresin yield FR. For viewing clarity, the direction of the FR axis is reversed between the two figures.

responses, however, do expose beetles to conditions that elevate the overall death rate. Disruption of the attack process lengthens the time a beetle is outside a host, thereby increasing the chance of beetle death (Coulson, 1980). Mortality of this nature is not treated in our analysis and, thus, is not a factor contributing to our results.

CONCLUDING REMARKS

Markov chain analysis can be used to study sequential behavioral processes, such as those involved in host selection by *D. front&.* This analysis provides information that cannot be obtained from observations alone or experiments that evaluate more limited aspects of the host selection process. The similarity of our predicted outcomes to the observations described by Bunt *et* al. (1980) suggests that Markov chain methods are appropriate for analyzing these and similar behaviors. On-bark behavior of ***D.*** *frontalis* is complex, exhibiting many states and potential transitions. A probabilistic approach to modeling such behavior is intuitively appealing because many of the state changes are necessarily stochastic, being dependent, for example, on the location of conspecifics, predators, and bark crevices.

The observations reported by Bunt *et* al. (1980) provide the empirical results necessary for analysis by Markov chains. Beetle activities were observed *in situ* and on-bark behavior of *D. frontalis* was partitioned into 12 categories, 8 transient states (LAND, SEARCH, WALK, PRED, SPB, FIGHT, PITCH, BORE) and 4 terminal states (FLY, DROP, EATEN, ENTER). Predictions generated from our chain analysis of observed transition data agree well with the terminal behavior frequencies reported by Bunt *et **al.*** (1980). Expected total numbers of beetle behavioral transitions after landing on a host tree, or following any other transitory behavior, also are available and can be used to identify behavioral tendencies that occur for the entire on-bark process or any desired portion of it. It is apparent that this analytical approach, made possible by data collection organized so that transition probabilities can be estimated, has advantages when a complex process with multiple outcomes is being studied.

The use of separate chains for male and female beetles facilitated study of sexual differences in on-bark behaviors. Results suggest that behavioral inclinations differ between the sexes, beyond the already recognized fact that beetles of each sex engage in some activities not common to the other. For example, the consequences of fighting differed between sexes, as males appeared to increase their chance of entering a host tree by fighting when they encountered a conspecific, while females benefited more from continued searching.

With a Markov chain model one can assess changes in probabilities of entering terminal states that occur as transition probabilities are varied. Differences in outcome probabilities that are induced by these changes indicate the sensitivity of a process to particular forms of variation, thereby identifying behaviors that critically influence process outcomes. For *D. frontalis*, independently increasing resin flow or predator density appears to lead to lower beetle penetration rates and increased beetle mortality. However, at high resin flow rates, increasing predator density leads unexpectedly to decreased on-bark mortality, a result that can be tested experimentally.

In conclusion, we believe that Markov chain analysis provides a framework for improving investigation of behavioral sequences commonly observed for insects. It focuses attention on probabilities of movement between behavioral activities and can be used to estimate probabilities of entering various terminal behaviors of a process. The analysis is sufficiently flexible to include additional information about host selection behaviors as it becomes available. For example, the effect of beetle lipid levels or the density of conspecifics (e.g., Wallin and Raffa, 2000, 2002) may be accommodated in Markov chain models once their effect on transition probabilities is determined. Experimental studies that concentrate on defining behavioral states and estimating transition probabilities among them, preferably *in situ*, allow the quantitative description and evaluation of entire processes. Such an approach contrasts with those that focus on results obtained from a small portion of a sequence or a single behavioral event. In a Markov chain framework, multistage processes with multiple uncertain outcomes can be investigated without disregarding emergent properties and behavioral redundancies that may be important in determining process outcomes.

APPENDIX A: ADDITIONAL ASSUMPTIONS

Under Markovian Analysis of On-Bark Behavior (above), we noted that in the Bunt *et* al. (1980) study, arriving beetles were 48.3% female and 51.7% male. Assumptions regarding female and male behaviors needed to develop separate transition matrices (Tables II and III) for each sex, using frequencies for the combined population contained in Fig. 2 and Table I, are as follows.

A1. Searchers (SEARCH-54% of the landers) are 48.3% female and 51.7% male. This is equivalent to assuming there are no sexual differences in transition probabilities among landed beetles, so the entries in row LAND in Table I apply to males and females separately.

A2. There are no sex differences in transition probabilities among walking beetles or those that encounter a predator, so the entries in rows WALK and PRED in Table I apply to males and females separately.

A3. According to Fig. 2, of those beetles engaged in SEARCH behavior
- 14% begin to BORE (as noted in the text, all these are female, so 29% of searching females begin to bore),
- 13% encounter another SPB (assume 13% of each sex),
- 19% leave (DROP, FLY, PRED-assume that proportions are the same for each sex), and
- 54% investigate entrance holes (PITCH-the preceding assumptions imply that 39% of the female searchers and 68% of the males enter this state; conversely, of those beetles that begin this activity, 35% are female and 65% are male). Note: These figures, and similar ones below, were obtained using standard techniques of conditional probability.

A4. Of the borers, all of which are female,
- 6% encounter a predator (PRED),
- 5% drown in host resin (DROWN), and
- 89% successfully penetrate the bark (PEN) to begin gallery construction and oviposition.

A5. Among ALL beetles that investigate an entrance hole (PITCH—from A2, 35% of these are female and 65% male), Fig. 2 indicates that
- 21% enter the hole (ENTER-all these are male, so 32% of the males enter the tree),
- 29% encounter another SPB (assume 29% of each sex),
- 2% drop off the tree (DROP-assume 2% of each sex), and
- 48% return to searching (SEARCH-the preceding assumptions imply that 37% of males and 69% of females follow this path).

A6. Of the beetles that encounter another southern pine beetle (from A2 and A4, 41% of these are female and 59% are male)
- 13% drop off the tree (DROP-assume 13% of each sex),
- 29% fight (FIGHT-assume that 90% of these are male and 10% female; equivalently, 44% of males fight, while only 7% of females fight), and
- 58% move to searching activity (SEARCH-the above assumptions imply that 43% of males, and 80% of females, that encounter another southern pine beetle will switch to searching).

A7. Of those beetles that FIGHT (from A6, 90% are male)

- 23% enter an existing hole (ENTER-all these are male, so 26% of the males that fight then enter a hole),
- 11% drop off the tree (DROP-assume 11% of each sex), and
- 66% move to searching activity (SEARCH—63% of the males and 89% of the females).

APPENDIX B: MODELING PREDATOR DENSITY

The effects of varying predator density shown in Fig. 3 were obtained by modeling density in *relative* terms. To establish a baseline, we assigned density $D = 1$ to the Bunt *et al.* (1980) study conditions. Probabilities associated with other densities were then computed using an assumption of stochastic independence.

For example, to obtain a transition matrix when $D = 2$, we postulated two predator groups, each with density $D = 1$, and assumed that the events E_1, a beetle evades all predators in the first group, and E_2, a beetle evades all predators in the second group, were independent. When $D = 1$, a beetle engaged in SEARCH behavior has probability 0.06 of encountering a predator (Table I) and, thus, probability 0.94 of evading all predators. The probability that it evades all predators when $D = 2$ (i.e., when events E_1 and E_2 both occur) is thus $(0.94)^2$, and the probability that such beetles encounter a predator is $1 - (0.94)^2$.

In general, when predator density is D, the probability that a searching beetle encounters a predator is $1 - (0.94)^D$. Other entries in the SEARCH row of the transition matrix were then adjusted proportionally so the new sum was 1.0, as required.

Similar procedures were followed for the other behavior categories, LAND, WALK, and BORE, in which beetles can encounter predators. Standard Markovian analysis of the resulting matrices produced the histograms in Fig. 3.

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