

Who goes first? Condition and danger dependent pioneering in a group-living bark beetle (*Dendroctonus ponderosae*)

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Abstract Among group-living organisms, some individuals initiate groups by being the first to attack a prey item or the first to colonize a new settlement site. In the group-living mountain pine beetle (*Dendroctonus ponderosae*), first attackers (known as pioneers) on live trees suffer higher mortality due to tree defenses than do beetles that join aggregations. This study examined factors that affect an individual's propensity to initiate an aggregation. When placed on an unoccupied tree, the probability of successfully entering the tree was positively correlated with body condition (residual of mass versus length regression). However, beetles in better condition took longer to initiate tunnel construction than those in poorer condition, suggesting that pioneering is a “desperation” strategy used when low energy reserves preclude further dispersal or when potential trees are rare. These contrasting patterns suggest pioneering is a nonlinear behavioral response, such that beetles with the smallest energy reserves and beetles with the greatest energy reserves both avoid pioneering. We further found that pioneering was more likely when the environment favored success, such as in smaller diameter trees (which may have weaker defenses) and earlier in the season (when the probability of recruiting conspecifics is higher). Our results suggest that pioneers incorporate both

internal and external variables in their decision to attack an uncolonized tree.

Keywords Pioneering · Joining · Social · Aggregation · *Dendroctonus ponderosae* · Habitat selection

Introduction

The formation of groups of animals requires individuals that initiate a group and ones that join it. Most attention has focused on the conditions under which individuals would join rather than be solitary (Giraldeau and Beauchamp 1999; Hamilton 2000; Prokopy and Roitberg 2001) in part because it is generally assumed that the best situation would be to monopolize resources alone. However, in some group-living animals, fitness increases as group size increases. This inverse density dependence is known as an Allee effect (Allee 1949). Examples include animals that forage on dangerous or difficult prey and those where reproductive opportunities depend on the number of conspecifics in close proximity. In such cases, the individuals that pioneer on a resource may suffer serious fitness consequences if others fail to join (Stander 1992; Toonen and Pawlik 1994). The question then becomes: under what conditions should an individual risk being the first to initiate a group?

In the present study, we use mountain pine beetles (*Dendroctonus ponderosae*, Coleoptera: Curculionidae, Scolytinae) to examine factors that may affect an individual's propensity to join or to initiate a breeding aggregation when reproductive success depends upon the recruitment of conspecifics. Breeding by mountain pine beetles occurs on trees (*Pinus* spp.) that are initially alive, and the first beetles that establish breeding sites on a host tree are termed the

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pioneers (Raffa and Berryman 1983). We will, henceforth, use the term “pioneer” to refer to the very first beetle to enter a previously uncolonized tree. Reproductive success in mountain pine beetles is contingent upon successful aggregation that terminates tree defenses and allows beetles to feed and reproduce, ultimately killing the tree (Raffa and Berryman 1983). Pioneering in bark beetles can be costly. Pioneer bark beetles may suffer high mortality rates (Raffa and Berryman 1983; Latty 2007), low probability of recruitment (54%, Raffa and Berryman 1983; 32%, Latty 2007), and low reproductive success (Pureswaran et al. 2006; Latty and Reid 2009). As a result, pioneering may represent the riskier, less desirable strategy relative to joining.

Despite the costs, some individuals must pioneer in order for an aggregation to form. How individuals make the decision to initiate aggregations instead of joining them is not yet known for the majority of aggregating species, including bark beetles (Raffa et al. 1993). An individual's energetic state may be influential, such that individuals with ample energy reserves should settle in higher quality habitats (Ward 1987; Stamps et al. 2005). Consequently, when fitness declines with group size, pioneers are expected to have greater energy reserves than joiners (e.g., Öst et al. 2003), while when fitness depends on being joined, it may be individuals with lower energy reserves that pioneer (initially proposed for colonial marine invertebrates as the “desperate larva” hypothesis by Knight-Jones (1953). Byers (1999) proposed that individual bark beetles would initiate aggregations only if the beetle's energy reserves were low and no aggregation pheromone (indicating active aggregations) was perceived. However, in laboratory studies, Wallin and Raffa (2000, 2002, 2004) found that bark beetles with greater lipid concentrations were more likely to enter artificial media amended with tree volatiles than were beetles with low-lipid levels. To our knowledge, the desperation hypothesis has not been tested in bark beetles under field conditions.

The costs of pioneering may be mitigated if pioneers preferentially initiate aggregations on “safe” settlement sites or by selecting sites that have a higher probability of attracting conspecifics. In this view, the occurrence of pioneering is influenced primarily by the settlement site's characteristics rather than by the pioneer's characteristics or state. Mountain pine beetles might make decisions about whether or not to accept an uncolonized tree by assessing tree defenses and avoiding those trees that pose a significant danger. Resin flow is a tree's first line of defense against insects and pathogens (Berryman 1972). Thus, avoiding trees with high resin flow could increase pioneer survivorship. Paradoxically, increased resin flow may also increase the probability of recruiting conspecifics. Female mountain pine beetles produce an aggregation

pheromone by metabolizing the tree monoterpene α -pinene to produce the aggregation pheromone *trans*-verbenol in a dose-dependent manner (Gries et al. 1990b), as has been observed in another bark beetle (Byers 1981). Increased resin flow could, therefore, increase pheromone production and result in greater recruitment success for pioneers (Raffa 2001). Overall, host-tree traits may influence the propensity to pioneer, but the direction of the relationship is more difficult to predict.

The propensity to pioneer could also be explained by the interaction between energetic state and site condition. Individuals could modify their pioneering decisions to account for individual susceptibility to the danger posed by particular settlement sites and to that posed by continued search (Byers 1999; Stamps et al. 2005). Individuals that are more likely to suffer high mortality when settling alone may choose to continue dispersing, while less susceptible individuals may choose to pioneer. Bark beetles with low energy stores may be less able to tolerate defensive monoterpenes produced by the tree in response to insect attack (Gries et al. 1990a, implied by their Fig. 4), and may have a harder time moving against the thick, viscous resin. As a result, smaller pioneers may face a higher chance of mortality. Thus, pioneers with lower energy reserves may readily enter an unoccupied tree with a low defensive response but may avoid trees with high defense responses because the risk of mortality in such a tree is greater than the risk of mortality through continued search. Pioneers with high energy reserves may be able to tolerate tree defenses and benefit from them, as previously discussed. This idea, which we refer to as the condition-matching hypothesis, predicts a positive interaction between pioneer energetic status and tree resin defenses in the propensity to enter an uncolonized tree.

In the present study, we examined two measures of beetle propensity to pioneer. We looked at whether or not a beetle entered the tree and then, for those that eventually entered, we examined the amount of time it took for them to make the decision to become a pioneer (by initiating tunnel construction). We examined three hypotheses to explain how pioneers make decisions about whether or not to pioneer by examining the effects of beetle energetic status (desperation hypothesis), tree characteristics (safe site hypothesis), and the interaction of beetle energetic status and site characteristics (condition-matching hypothesis).

Methods

The mountain pine beetle is an eruptive species that periodically kills millions of mature lodgepole pine (*Pinus contorta* Douglas var. *latifolia*) in much of north-western North America (Safranyik and Carroll 2006). Individual

female mountain pine beetles initiate breeding sites within the phloem (inner bark) of trees where they feed and reproduce. Once inside the phloem, beetles begin producing aggregation pheromones that attract conspecifics of both sexes. In order for beetles to reproduce within a tree, they must exceed densities of 40 beetles per square meter (for an average lodgepole pine) to overwhelm tree defenses (Raffa and Berryman 1983).

The study was conducted in the summer of 2004 at sites in Banff and Kootenay National Parks in areas that were experiencing outbreaks of mountain pine beetles. These parks abut at the border of southern Alberta and British Columbia, Canada. One site was selected in Banff (Mt. Norquay: 51°11'31" N, 115°35'26" W) and two were selected in Kootenay: Dolly Varden (50°49'26" N, 116°00'34" W) and Mt. Wardle (50°56'51" N, 115°59'36" W). Trees at the Banff site had a mean age of 84 years (± 3.0 SE) while trees at the Kootenay site had a mean age of 91 years (± 19.0 SE) from tree cores taken at breast height. Kootenay has had multiple large outbreaks over recorded history, while outbreaks in Banff have been rarer and smaller due to the less hospitable climate.

To obtain experimental beetles, bolts of trees colonized by mountain pine beetles were cut from naturally colonized trees in Banff National Park and placed into emergence containers in the lab. Beetles were collected upon emergence whereupon female beetles were randomly assigned to two treatment groups: starved and nonstarved. The starvation treatment aimed to increase the range of energetic condition among beetles, similar to what might be expected after a period of dispersal (Gries et al. 1990a; Williams and Robertson 2008). Nonstarved beetles were stored at 4°C immediately upon emergence to lower their metabolism and prevent fat loss until used in experiments. Starved beetles were left at room temperature for 5 days and then stored at 4°C until used. Beetles were stored individually in 10 ml vials with moist tissue. After treatment, each beetle was weighed to the nearest 0.1 mg. Body length (tip of head to posterior end of elytra) was measured to the nearest 0.1 mm using a dissecting microscope fitted with an ocular micrometer. From these values, we calculated a residual index of body condition that is a good indicator of energetic status in a wide range of organisms (Schulte-Hostedde et al. 2005). Body condition was calculated by regressing the mass of our nonstarved beetles by their length ($\text{mass (mg)} = -0.02 + 0.008 \text{ length (mm)}$, $N=500$) and taking the residuals. Positive residual values indicate beetles that weighed more than expected for their body size while negative values indicate individuals who have lower than average mass to length ratios. We assume that higher residual values indicate better body condition (Schulte-Hostedde et al. 2005). We used nonstarved beetles in our regression, and the body condition of starved beetles was determined as the

difference in their mass from that expected for their length given our regression.

To test the propensity of females to initiate tunnel construction in uncolonized trees, we used a procedure similar to that used by Raffa and Berryman (1983). Study beetles were placed individually on the north side of selected lodgepole pine trees within clear plastic containers with ventilation holes. These containers, 12 cm in diameter, prevented beetles from escaping but allowed them some choice in their entrance behavior. Placements were conducted between 27 June and 2 August, spanning the majority of the mountain pine beetle flight period in these areas (TM Latty, personal observation, based on captures from emergence traps). There is evidence supporting the hypothesis that mountain pine beetles land on trees randomly, and then make tree acceptance decisions based on olfactory and/or gustatory cues (Hynum and Berryman 1980; Moeck et al. 1981; Pureswaran and Borden 2003). Thus, placing beetles directly on the bark surface is an appropriate way to assess postlanding tree acceptance. Lodgepole pine trees were selected for this experiment based on the following criteria: they had a diameter at breast height (diameter) greater than 20 cm, appeared to be in good health (green needles, no physical damage), and had no signs of previous mountain pine beetle attack.

After beetles were placed on trees, they were checked every 2 h for the first 6 h after which time beetles were checked once every 24 h (at ~1100 h) for the following 3 days. At each check, beetles were classified as (a) initiating tunnel construction; (b) not initiating tunnel construction but still alive on bark surface; (c) dead; or (d) escaped. Tunnel construction was considered to have started when bark fragments from boring were clearly visible, and the beetle had all or part (>50%) of its body wedged into the nascent tunnel.

On the third day following beetle placement, we took resin flow measurements using a modification of Mason (1969). We drilled three 2 mm holes, 1.5 cm into the tree and inserted a 2-ml pipette tube into each hole at a slight upward angle. The three tubes were placed in each tree 5 cm apart, on the north side, approximately 10 cm below the beetle. After 24 h, the volume of exuded resin was measured in each of the three pipettes and averaged. Lodgepole pine trees can respond to the presence of insects or pathogens by increasing resin flow to the infected area, necrotizing tissue surrounding the wound site, and by synthesizing defensive monoterpenes (Berryman 1972). Measuring resin flow 3 days after beetle placement allowed us to capture the tree's response (if any) to the beetle's presence, as induced responses appear to predict tree suitability better than constitutive defenses (Raffa and Berryman 1982).

All the previously mentioned work was conducted on trees that had no beetles other than our experimental one. We also examined the effect of body condition on beetle propensity to join established aggregations that developed on some of our experimental trees. Joiner beetles were placed on trees between 15 July and 2 August using the same procedure previously described with a few modifications. Joiners were placed on trees where an experimentally added female had successfully initiated mass attack by recruiting conspecifics. Joiners were placed in enclosures on the tree within 2 days of the tree reaching optimal density (60 beetles per square meter, Raffa and Berryman 1983). These beetles were then checked according to the schedule previously described.

Data analysis

To test our three hypotheses on the propensity to pioneer, we created a logistic regression model with entered versus not entered as the binomial dependent variable. Our central independent variables of interest were body condition, site, resin flow, and an interaction between resin flow and body condition. Initial models also included average temperature, tree diameter, and placement date as covariates, but these were removed from the final models if they were found to be nonsignificant. Average daily temperature was included to control for the possibility that entrance time might be influenced by ambient temperature because mountain pine beetles are ectothermic. Average daily temperature data came from weather stations located in Banff and Kootenay National Parks. Temperature on placement day was recorded every hour and then averaged over 24 h for the appropriate site starting at 1,100 h on the day of implantation. Preliminary analyses found no difference between the two sites in Kootenay, so these sites were grouped together.

The time it took for a pioneer to initiate tunnel construction was analyzed using a multiple regression model with tunnel initiation time (hours; ln-transformed) as the dependent variable and the same independent variables and model building procedure previously described for the logistic regression. For joiners, we examined entrance behavior (entered versus not entered, time until tunnel initiation) with only body condition as the independent variable because of our limited sample size.

Preliminary analyses of our data revealed an outlier: a beetle whose body condition was much higher than all other beetles (Fig. 1), but whose length and width appeared normal. After careful scrutiny of the raw data, we failed to find any a priori reason to exclude the outlier from the analysis. Nevertheless, the beetle's high body condition was clearly disjunct from that of our other experimental beetles. We were unable to confirm the beetle's measurements, so it

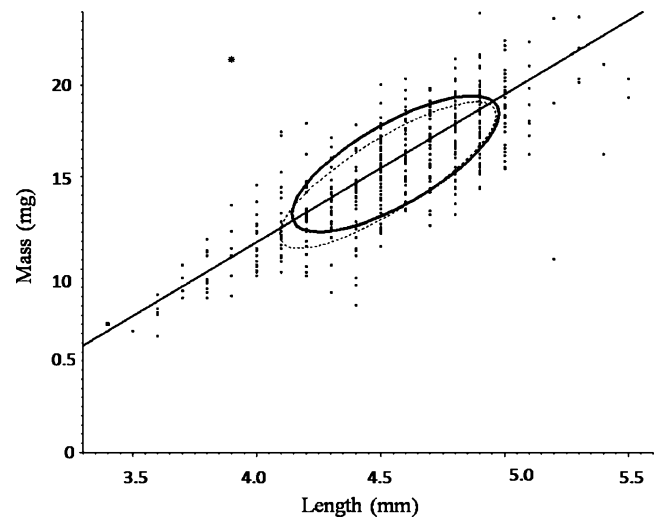


Fig. 1 Plot of beetle mass versus length. The *solid gray regression line* shows the result of a regression of beetle weight by length for unmanipulated, nonstarved beetles. Individuals *below* this line have lower than average body condition; individuals *above* the line have higher than average body condition. The *solid ellipse* shows 50% confidence intervals for beetles that successfully entered the tree. The *dotted ellipse* shows 50% confidence intervals for beetles that did not enter the tree. The *asterisk* denotes the outlier

is possible that the beetle was incorrectly measured. The beetle's inclusion had important effects on our results. As a consequence, we present our results both including and excluding the outlier. Means are presented with the outlier excluded unless otherwise stated.

For all linear regression models, residuals were examined after model fitting to ensure that assumptions of homoscedasticity and normality were met. Variance inflation factors (VIFs) were checked to ensure that the assumption of independence of variables was also met. VIFs greater than ten indicate strong collinearity (Quinn and Keough 2002). Variables were, therefore, conservatively rejected if they had a VIF greater than five. We further removed nonsignificant covariates (that did not test our focal hypotheses) sequentially in the order of least significance. All statistical analyses were performed using JMP 7.0 (SAS Institute). All means are reported \pm SE unless otherwise stated.

Results

Entered versus not entered

Overall, 52% of 257 beetles entered uncolonized trees. Beetles had a mean body condition of 0.5 ± 0.1 mg. Beetles in better condition were more likely to enter trees than beetles in poorer condition (Table 1, Fig. 1), and this effect persisted when the outlier was included. Resin flow had no detectable effect on the probability of entrance, and there was

Table 1 Results of the logistic regression model for beetle entrance (entered versus not entered)

Variable	Coefficient estimate	χ^2	P	
Body condition (mg)	0.168	5.11	0.04 ^a	(0.01) ^a
Resin flow (ml/24 h)	0.48	1.53	0.21	(0.22)
Resin flow \times body condition	-306.81	1.97	0.21	(0.21)
Site	0.21	1.84	0.17	(0.17)
Tree diameter (cm)	-0.09	5.10	0.02 ^a	(0.03) ^a
Placement date	-0.047	4.86	0.03 ^a	(0.02) ^a

Values are taken from the model in which the outlier point has been excluded; values in brackets are from the model which included the outlier
^a P values are significant at the 0.05 significance level; $n=256$ (257 including outlier)

no detectable interaction between beetle condition and resin flow in determining the likelihood of entering (Table 1). Site did not have a detectable effect on whether or not beetles entered trees. Beetles were more likely to enter smaller diameter trees (Table 1); thus, for trees smaller than the median size (20.0 to 28.5 cm diameter), 61.9% of beetles entered, while 54% of beetles entered larger trees (28.6 to 38.0 cm diameter). Placement date also had an effect on whether or not beetles entered trees such that beetles were more likely to enter trees if they were placed on trees early in the season (Table 1). Early in the season (27 June to 1 July), 63% of beetles entered their trees, while later in the season (12 July to 2 August), 58% of beetles did so.

Entrance time

On average, pioneers took 34.7 h to initiate tunnel construction (95% CI=30.95–38.45 h, $n=228$) with 20% initiating tunnels in less than 2 h. Pioneers in poorer body condition tended to initiate tunneling sooner than those in better condition regardless of whether or not the outlier was included (Table 2, Fig. 2). With the outlier included, there

Table 2 Results of linear regression model of time until entrance

Variable	Coefficient estimate	F	P	
Body condition (mg)	0.134	2.43	0.02 ^a	(0.048) ^a
Resin flow (ml/24 h)	-226.21	1.16	0.24	(0.33)
Resin flow \times body condition	0.26	-1.47	0.14	(0.02) ^a
Site		2.26	0.02 ^a	(0.02) ^a

Values are taken from the model in which the outlier point has been removed. P values in brackets are from the model which included the outlier

^a P values are significant at the 0.05 significance level; $n=159$ (160 including outlier)

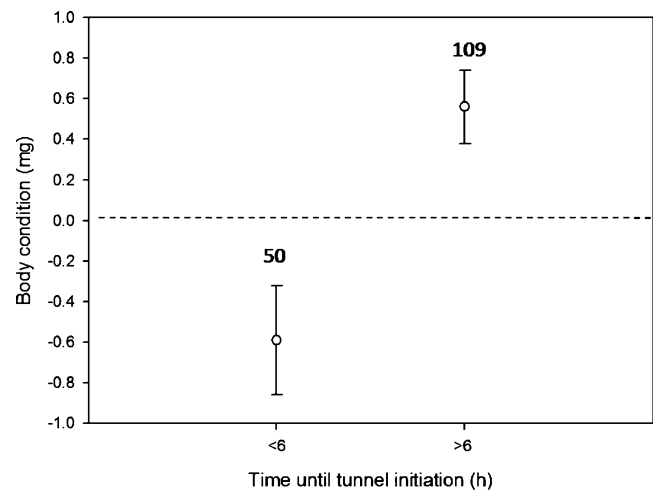


Fig. 2 Mean body condition (\pm SE) of beetles that entered sooner (in <6 h) and later (>6 h; $P=0.0004$, $F=12.844$, $n=159$, analysis of variance), as classified for presentation. The numbers *above the bars* show sample sizes, and the *dashed line* indicates the expected condition value of zero. Note that dependent and independent variables have been reversed for ease of interpretation

was a significant positive interaction between body condition and resin flow, suggesting that females in better body condition initiated tunneling in trees with more resin sooner than did females in poorer condition (Table 2). However, this interaction was no longer significant when the outlier was removed (Table 2). Resin flow on its own did not have a significant effect on tunnel initiation in either model (Table 2). In both models (with and without the outlier), site had a significant effect on tunnel initiation such that pioneers initiated tunnels sooner at the Banff site (24.5 ± 1.1 h) than at the Kootenay sites (14.8 ± 1.2 h; Table 2).

Effect of body condition on joiner entrance

Of 23 joiners, 73% entered trees. Joiners had a mean body condition of 0.3 ± 0.3 mg. The mean entrance time (back-transformed) for joiners was 4.4 h (95% CI=2.9–6.7 h, $n=17$). Body condition had no detectable effect on a joiner's propensity to enter trees ($\chi^2=0.28$, $P=0.1$, $n=23$) or on its entrance time ($R^2=0.007$, $P=0.4$, $n=23$).

The body condition of joiners was not significantly different from the body condition of pioneers (two-tailed t test: $t=-1.20$, $P=0.2$, $n=288$).

Discussion

Our results suggest that the decision to pioneer is complex and conditional, with some support for all three of our hypotheses (desperation, condition-matching, and safe site) under some circumstances.

Body condition

Among pioneers, body condition predicted entrance behavior, but the effect was inconsistent between our two measures of propensity to enter. Beetles in better condition were more likely to enter trees than those in poorer condition, but among those that entered, beetles in poorer condition generally initiated tunnel construction sooner. Thus, our results suggest that there is a nonlinear effect of body condition on propensity to pioneer. It should be noted, however, that the difference in body condition between beetles that entered and those that did not is quite small (Fig. 1). This suggests that the effect of body condition on the probability of entering a tree is relatively subtle.

The lower propensity of beetles in poorer condition to enter trees, relative to those with higher condition values, could result from either physical inability or choice. Beetles in poor condition may lack the energetic reserves to initiate gallery construction, resulting in a lower overall probability of entering trees. Low energy reserves have been associated with entrance failure in lab experiments (Wallin and Raffa 2000; Elkin and Reid 2005). However, the body condition of beetles that died tended to be lower than those that did not enter, suggesting that our results are not solely a consequence of moribund beetles. Further, body condition had no effect on the propensity of beetles to enter colonized trees (joiner beetles), suggesting that low poor body condition beetles are still physically capable of entering trees.

Alternatively, beetles with very low energy reserves may choose not to pioneer due to the high probability of death in the face of undiminished tree defenses. Beetles with lower energy reserves may have difficulty tunneling against resin flows. As a result, beetles have lower energy reserves and so have a low chance of surviving tree defenses might avoid pioneering and settle instead in mass-attacked trees with depleted defenses resulting in a lower overall probability of entering uncolonized trees compared to beetles with relatively full energy reserves. This finding appears to support the condition-matching hypothesis. We had suggested that the condition-matching hypothesis predicts an interaction between body condition and resin production, such that beetles in poor condition would prefer poorly defended trees while beetles in good condition would prefer more defended trees. There was a hint of such an interaction when considering the speed with which beetles initiated tunnels, but only when an outlier was included in the analysis (Table 2).

For beetles that entered the tree, body condition had a significant effect on the speed at which individuals initiated tunnels, but opposite to the results for the probability of entering: beetles in poorer condition tended to initiate tunnels sooner than did beetles in better body condition. Beetles with initially high energy reserves presumably

postponed initiating tunnel construction until their energy reserves fell below some threshold. This supports the desperation hypothesis (*sensu* Byers 1999). Individuals with higher energy needs often incur higher predation risk to obtain resources (Lima and Dill 1990), and foragers are predicted to become less choosy as their energy reserves deplete (Byers 1999; Stamps et al. 2005). Similarly, beetles may be trading off the mortality risk of pioneering against their energetic requirements and the risk of continued search. However, as previously noted, this trade-off may apply over a limited range of body conditions, with the beetles in the poorest condition unable to realize a net gain in trees harboring some defenses and therefore avoiding entering at all.

Environmental factors

Pioneers were more likely to enter smaller diameter trees than larger ones, and more likely to enter trees early in the season than later. These results suggest that the probability of successful breeding influences the probability of pioneering. The greater propensity to enter smaller trees may be driven by an attempt to avoid trees with higher defensive capabilities. Pioneers could prefer small trees if small trees have lower defensive capabilities (e.g., lower levels of monoterpenes, less viscous resin) than larger trees. Among our trees, we detected no direct effect of resin flow or a relationship between resin flow and tree diameter (not shown), though Nebeker et al. (1995) found a positive relationship between resin flow and tree diameter in a stand in Wyoming, USA. Alternatively, beetles may have had greater difficulty entering larger trees because these tend to have thicker outer bark as seen in another pine bark beetle system (Kolb 2006).

The preference for smaller trees by pioneers contrasts with general observation that trees killed by mountain pine beetles tend to be the larger ones of those available, consistent with pattern that reproductive success increases with tree diameter (Safranyik and Carroll 2006; Raffa et al. 2008). However, in endemic (low) populations of mountain pine beetles, mass-attacked trees tend to be smaller than those available (Safranyik and Carroll 2006). Our results point to the process that may lead to these patterns. Pioneer beetles may always be more likely to enter smaller trees, but recruited beetles may be more likely to settle on larger trees because of their greater surface area (Hynum and Berryman 1980) and prospects for reproductive success. In small populations, recruitment may be sufficiently slow or rare that pioneers on larger trees fail before others are recruited, causing smaller trees to be more likely to be mass-attacked.

The lack of a detectable direct relationship between pioneer entrance behavior and resin flow could arise for

several reasons. Resin flow is only one component of a tree's defensive systems, and factors such as resin crystallization rate, monoterpene composition or concentration, or other defense components may be better indicators of a tree's defensive potential that pioneers could use to judge the danger posed by a tree (Seybold et al. 2006). Increased concentrations of the monoterpene α -pinene decreased entrance behavior by *Ips pini* on artificial media (Wallin and Raffa 2000). It could also be that the timing of our measurements of resin flow, 3 days after the test, did not capture the information available at the time of potential pioneering. Induced defensive responses appear to be more critical than constitutive defenses for tree resistance (Raffa and Berryman 1982, 1987), but we do not know what cues beetles use to predict tree defensive responses to the beetles' entrance. Field studies are needed to examine how other defensive characteristics (such as monoterpene concentrations) influence the propensity to pioneer under field conditions.

The greater likelihood of pioneering early in the season than late in the season also suggests that females pioneer when the risk of failure is lower. Early in the season, pioneers have a greater amount of time to potentially recruit conspecifics and pioneers that fail to recruit conspecifics after some time period could still re-emerge in time to search for potential trees. Later in the season, the probability of attracting enough conspecifics to form an aggregation is likely much lower (Bentz 2006). In addition, late-settling pioneers are unlikely to re-emerge (Latty 2007), presumably because the remaining search time is too short to make finding a new tree likely. Thus, the effect of placement date appears to be driven by the pioneer's need to recruit conspecifics and the likelihood of it being able to locate a new tree should it re-emerge.

Taken together, our results tentatively support the safe site hypothesis. Beetles may be selecting trees with low defenses, as suggested by their response to tree diameter. Further, they are more likely to pioneer at the time of season that maximizes their probability of recruiting conspecifics and/or finding a new tree should the pioneering attempt fail. This is not necessarily a process that is incompatible with condition-dependent pioneering, but rather an additional contributor to the net benefits of pioneering on a particular tree.

In sum, our results highlight the complexity of decision making in mountain pine beetle. Ultimately, the decision to initiate an aggregation is complex, involving multiple, interacting factors. This is perhaps unsurprising given the large number of factors that can affect the success of a pioneering attempt. Our study has revealed several important factors affecting the decision to initiate an aggregation in mountain pine beetles, but there are many other factors that remain unexplored. Similarly, we expect that aggrega-

tion initiation decisions in other species will be equally complex.

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