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'To tree or not to tree': the role of energy limitation on host tree acceptance in a bark beetle

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ABSTRACT

Background: Energy and time constraints experienced by dispersing animals often limit individual dispersal and subsequent habitat selection decisions. When substantial variation in individual dispersal capability is present, these constraints may have significant impacts on populations where condition-dependent evaluation of habitat sites interacts with state-dependent habitat selection. Latty and Reid (2010) hypothesize that the internal state of the dispersers and characteristics of their habitat mediate habitat selection ('condition matching').

Hypothesis: Individual beetles in better energetic condition are more likely to attack better-defended trees (i.e. riskier habitat).

Organism: Mountain pine beetle (*Dendroctonus ponderosae* Hopkins).

Field sites: Two field sites were used, and work at both sites coincided with the start of the beetles' emergence and flight period. Beetles used for lipid extraction analysis were collected near Merritt, BC, Canada in 2006, and host tree acceptance experiments were performed in 2010 near Field, BC, Canada.

Methods: We sampled a population of beetles to characterize the relationship between beetle size and lipid content, then examined the variation in individual somatic energy condition and date of emergence. We separately tested the effect of somatic energetic condition on habitat (host) selection decisions by experimentally manipulating beetles' somatic energy reserves, placing them on host trees of different nutritional qualities, and measuring the latency in beetles' host tree acceptance.

Results: Most beetles emerged early. Their somatic energy condition is higher at the start of the emergence period than near the end, although there is substantial individual variation in both timing and condition upon beetle emergence. Beetles' host selection decisions are influenced by both host tree nutritional quality and individuals' lipid reserves. Trees of good nutritional quality are accepted sooner than ones of poor nutritional quality. Individuals with lower energy reserves are less selective, accepting host trees of poorer quality sooner than beetles with higher energy reserves.

Keywords: dispersal, host selection, state-dependent behaviour, condition-dependent behaviour, bark beetles, *Dendroctonus ponderosae*.

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INTRODUCTION

Understanding the drivers of population-level distribution patterns of organisms is important for the conservation and management of species. How organisms distribute themselves across habitats reflects the outcome of habitat selection decisions by individual organisms, and is driven by individuals' assessment and evaluation of available habitats. For many organisms, the location and productivity of habitats varies both spatially and temporally, which poses additional challenges for dispersers as they search for and subsequently evaluate ephemeral habitat sites. Models of dispersal and habitat selection have generally considered populations of identical individuals, or used an 'average' behaviour extended to the whole population, thus ignoring the importance of individual behaviour, and individual variation, in determining population-level outcomes (Roitberg and Mangel, 1997; Patterson *et al.*, 2008; Clobert *et al.*, 2009).

In addition to site resources, several other important factors drive individuals' habitat settlement decisions. These decisions often account for extrinsic, environmental factors such as mortality risk (i.e. due to predators or host plant defences), as well as intrinsic factors such as a dispersing organism's energetic or other physiological state. Dispersing individuals are often limited in their energetic reserves as well as the amount of time available for habitat search and colonization. Thus, in many dispersing organisms, habitat selection decisions are limited by both energy and time constraints during dispersal (e.g. Ward, 1987; Stamps *et al.*, 2005). In species that disperse from their natal habitats, which includes many insect species, we observe substantial variation in both timing of emergence and somatic energetic condition at emergence. For such species, in order to predict population distributions, we must account for individual variation in energy stores and time available for search and the effects of these constraints on individual habitat selection.

This study examines the individual variation in energy (lipid) reserves at emergence, and the effect of lipid reserves on the host tree acceptance of the mountain pine beetle (*Dendroctonus ponderosae* Hopkins). The mountain pine beetle is a major forest pest, whose reproduction is contingent on successful attack and subsequent death of its primary host, lodgepole pine (*Pinus contorta* var. *latifolia*). Adult beetles overwhelm host tree defences (resin flows and monoterpene production) through the introduction of mutualistic blue-stain fungus, which is pathogenic to the tree, and by using a coordinated mass attack, which is initiated by individual beetles and mediated via pheromone cues produced by the attacking beetles. The timing of this attack is synchronous: early arrivals' entry into the host is slowed by the tree's defences (Raffa and Berryman, 1983), whereas beetles arriving mid-attack or later experience easier tree entry (Pureswaran *et al.*, 2006). Beetles arriving too early, before the attack is well underway, or who arrive too late, suffer reduced offspring production (Pureswaran *et al.*, 2006). Selection for synchrony in the timing of attack may also drive the evolution of synchrony of timing of emergence.

The decision to initiate an attack is based, in part, on host tree nutritional quality, tree defensive capabilities, and the density of conspecifics (Safranyik and Carroll, 2006). Individuals base their decisions on the perceived (mortality) risk at the selected site [i.e. the 'safe-site hypothesis' (Frank and Leggett, 1982)]. In this case, individuals are expected to select host trees that are less well defended by resin or that can be more easily overcome by a mass attack of beetles. Additionally, an individual beetle's energy reserves may influence host attack (acceptance) decisions (e.g. Atkins, 1966), in that beetles with higher energy reserves could afford to be choosier when selecting a host tree whereas those with low reserves would be more likely to accept hosts of poorer nutritional quality if host options are limited (Chubaty *et al.*, 2009; Latty and Reid, 2010). This is because those individuals with higher lipid content are expected to survive longer (e.g. Safranyik, 1976), have higher capacity for flight (Williams and Robertson, 2008), and therefore dispersal, and be better able to deal with the host's defences. Consequently, they would be more likely to find and attack more suitable (i.e. higher nutritional quality) hosts.

The extent to which host acceptance decisions by mountain pine beetles are based on energy reserves has not previously been tested directly in a field setting. If individuals select sites of low nutritional quality out of desperation, settling as a result of depleted energy reserves [i.e. poor somatic energetic condition; cf. the 'desperate larva' hypothesis for marine invertebrates (Knight-Jones, 1953)], then we would expect to see beetles in poorer energetic condition accepting trees of lower nutritional quality more often (and sooner) than beetles in better energetic condition, irrespective of the tree's defensive capabilities. Latty and Reid (2010) use the term 'condition matching' to describe an integrated hypothesis of habitat selection in the mountain pine beetle, which takes into account the influence of both host defences (i.e. site safety) and an individual's energetic state, whereby individuals in better energetic condition are more likely to attack better-defended trees, as also indicated in Chubaty *et al.* (2009).

The aims of this study are twofold. First, we determine the extent of individual variation in somatic energetic condition present in a field-collected population of mountain pine beetles. We measure the energetic condition of newly emerged beetles in relation to the timing of emergence, which may be important in determining the energetic status of individuals (e.g. late emergence is often associated with low energy reserves). Second, we test the role of energy (lipid) reserves on host tree acceptance of individual beetles in a field setting, and discuss the importance of considering individual variation and its impacts on individual behaviour and population dynamics.

METHODS

Field sites

Two field sites were used: the first, during the summer of 2006, to collect beetles on which to perform lipid analyses to determine energetic condition upon emergence; the second, during the summer of 2010, to run host-acceptance experiments. The beetle-collection site, located ~30 km south of Merritt, BC, Canada (49°50′15″N, 120°45′30″W) was a uniform, mature (≥80 years) lodgepole pine forest, in an area undergoing a widespread infestation of mountain pine beetle at the time. Experiments were conducted in Yoho National Park, near Field, BC, Canada (51°22′45″N, 116°30′48″W), in an area previously impacted by a mountain pine beetle outbreak. Work at both sites was conducted near the start of the beetles' emergence and flight period.

Condition upon emergence

Three large (diameter at breast height, DBH > 30 cm), beetle-infested lodgepole pine trees were felled in June 2006 and cut into 50 cm bolts. Bolts were stored in a refrigerated storage facility and kept near 4°C, until they could be transported back to the lab at the end of the field season (late August). Once back in the lab, bolts were placed into individual emergence cages and kept at room temperature. Emergence cages were checked twice daily: in the morning and late afternoon, and all emerged beetles collected and immediately frozen. Cages were monitored for 6 weeks after emergence began to ensure all emerging adult beetles were captured.

Beetles were individually sexed (see Lyon, 1958), and had their right elytron carefully removed and placed beside a stage micrometer (OB-M-2/200, $d = 0.001$ mm) under a dissecting microscope and photographed. The length (l) and width (w) of each elytron were then measured using imaging software (Rasband, 1997), and used to calculate a beetle size index using the formula for cylindrical volume, $v = \pi w^2 l$, as beetles are approximately cylindrical in shape. Beetles and their elytra were then individually sealed into filter paper envelopes and placed in a drying oven at ~62°C for 72 hours, before being weighed (Mettler Toledo XP26, $d = 0.001$ mg). Next, lipids were extracted using petroleum ether in a Soxhlet apparatus for 8 hours, after which time the samples were re-dried in the drying oven for 24 hours and reweighed, to determine the mass of lipids lost during the extraction. This corresponds to the lipid mass of the beetle (Elkin and Reid, 2005; Williams and Robertson, 2008).

Host acceptance experiment

Four lodgepole pine trees (approximately 25–30 cm diameter), heavily infested with mountain pine beetles, were felled, and several bolts (~40 cm) were cut from the bottom 3 m of each tree. These bolts were placed inside specially constructed containers to collect beetles as they emerged. These emergence containers were checked daily for beetles that were collected, brought back to the lab, and haphazardly assigned to one of the treatment groups: either in the fridge (~4°C) or at ambient outdoor air temperature (up to ~25°C) for 48 hours (e.g. Latty and Reid, 2010) on a substrate of damp paper towel. Because insects are ectotherms, beetles at higher temperatures expend their energy reserves more quickly than those at cooler temperatures. Therefore, beetles kept at ambient temperatures comprised the 'low-energy' group, and those stored in the fridge made up the 'high-energy' group. Approximately 20 beetles from each group were used, per experiment, on each test tree (several beetles died during the trials and were excluded from analyses). Beetles of both sexes were used due to the difficulty of accurately sexing live beetles using auditory and morphological characteristics, and to ensure large enough experimental cohorts.

To prepare trees for the experiment, suitable lodgepole pine trees were first identified based on canopy volume, proximity to neighbouring trees, diameter at breast height, and phloem thickness (PT). Phloem thickness was measured using a small circular punch and taken at breast height (~1.3 m) from the north and south sides of the tree. We selected four trees, from each of two classes. Trees of poor nutritional quality were smaller trees with thinner phloem (DBH: ~15–20 cm; PT: ~1 mm), while trees of good nutritional quality were larger and had thicker phloem (DBH: ~25–30 cm; PT: >1.5 mm). This characterization of tree nutritional quality classes is consistent with the lodgepole pine distributions in a previous study (Chubaty *et al.*, 2009). Trees within each class had approximately equal canopy volume and proximity to neighbouring trees based on visual assessment. Trees were girdled near the base approximately 36–48 hours before the experimental trials began to elicit a chemical response to the damage [which beetles find more attractive (Gara *et al.*, 1984)] and to partially mitigate the effect of host tree defences on beetles' choices. An area of the bark above the girdle (~1 m^2) was covered in mesh to prevent the experimentally introduced beetles from flying away, and to exclude non-experimental beetles. The mesh was wrapped loosely around the tree, tightly secured at the top and bottom using staples and duct tape, leaving a resealable flap through which observations could be made. Modelling clay was used to fill in gaps in the bark where the mesh was secured.

Before introducing the experimental beetles onto the trees, the rear portions of their elytra were coloured using brightly coloured (fluorescent) water-based paint (Crayola) such that beetles from the two experimental treatments were a different colour. All beetles were placed in a flight cage in the sun for ~2 hours to warm up and fly around in order to make them more receptive to attacking a tree. After this warm-up period, beetles from each treatment were introduced onto the experimental trees via the resealable mesh flap at the bottom of the experimental area on the western side of the tree. The time to attack (i.e. the time until each beetle began burrowing into the bark to begin gallery construction) was measured, along with the vertical distance along the bark the beetle moved prior to initiating gallery construction. Experiments were run until all beetles had entered the tree, up to a maximum duration of 3 hours.

At the end of the experiment, beetles were recovered from the tree so that lipid extractions (as described above) could be performed to confirm the temperature treatment generated the desired differences in the beetles' somatic energy condition.

Data analyses

The goal of the preliminary analyses was to determine the relationship between lipid mass and beetle volume, so that a size- and sex-corrected measure of lipid content (i.e. energetic condition) could be used in subsequent analyses (e.g. Jakob *et al.*, 1996; Elkin and Reid, 2010; Latty and Reid, 2010). Using a generalized linear model (GLM), lipid mass was examined as the response variable, with beetle volume, beetle sex, a volume × sex interaction, and the tree from which the beetle emerged as the predictor variables. A GLM was used instead of a generalized linear mixed model (GLMM) because there were only three different levels for the *tree*, thus *tree* could not be included as a random effect and was treated as a fixed effect in the model (Zuur *et al.*, 2009). This GLM was modelled using gamma-distributed errors with a log-link function, and showed significant sex and tree effects (Fig. 1; Table 1). The residuals from these models were used as a measure of beetle energetic condition for subsequent analyses for each sex.

To examine the relationship between date of emergence and energetic condition for each sex, we performed a bootstrapped ($N = 10{,}000$) cubic polynomial regression using higher-order *day* terms. Beetle timing of emergence was fit to a Weibull distribution, which describes poikilotherm emergence patterns (Wagner *et al.*, 1984). Additionally, by plotting these

Table 1. Generalized linear model of lipids mass vs. beetle volume

	Estimate	S.E.	*t*-value	*P*-value
(*Intercept*)	0.9441	0.0357	26.46	<0.001
Volume	0.0184	0.0019	9.78	<0.001
SexM	−0.1389	0.0533	−2.61	0.0092
TreeB	0.0851	0.0160	5.32	<0.001
TreeC	−0.0427	0.0160	−2.67	0.0075
Volume × S*exM*	0.0081	0.0033	2.42	0.0156

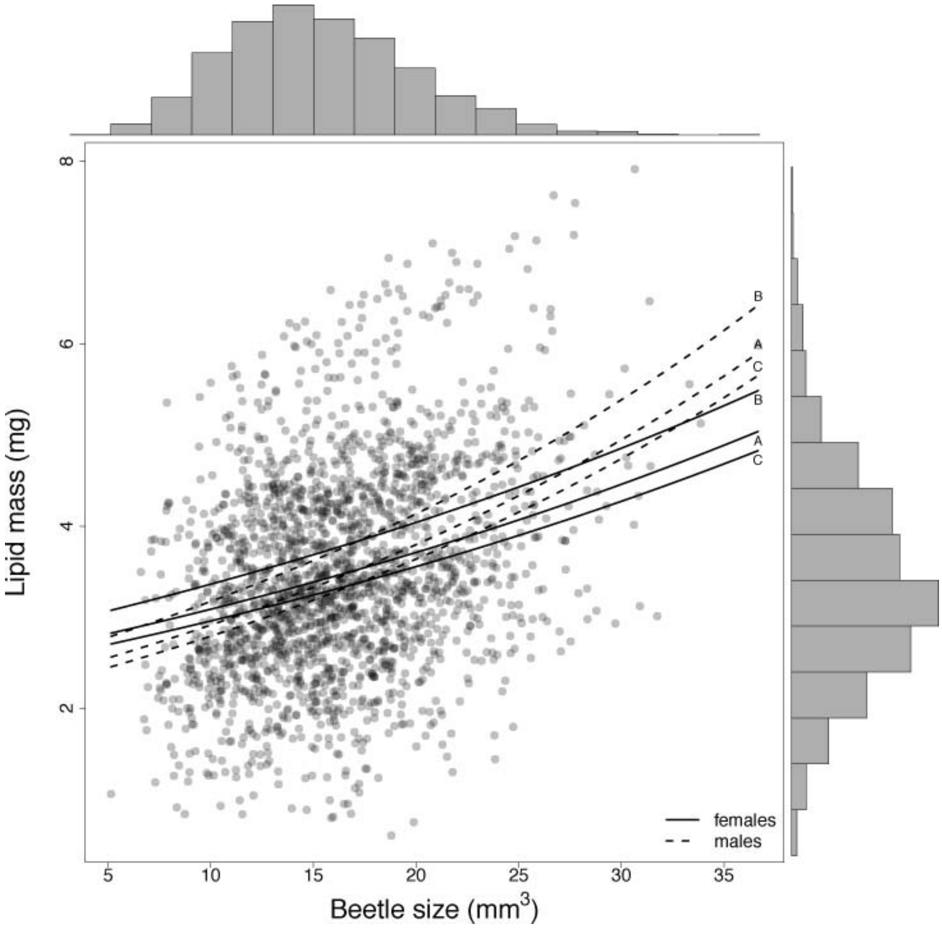

Fig. 1. Generalized linear model of beetle lipid mass with beetle volume for beetle sex and tree from which the beetle emerged; modelled using gamma-distributed errors with a log-link function. Residuals from this model were used as a measure of beetle energetic condition for subsequent analyses. Letters label curves corresponding to each tree. Histograms along each axis show distributions of the data.

emergence patterns against the proportion of beetles that emerged each day, we generated condition upon beetle emergence (CUBE) profiles, which represent the probability of a beetle emerging on a particular day with a particular energetic condition.

Experimental treatments were compared using analysis of variance (ANOVA), to assess the efficacy of our temperature treatments. A GLM model was used to determine beetle energetic condition, as above but without including *sex* and *tree*, which were non-significant. Beetles that had died during the experiment were excluded from analyses.

Latency (time until host tree acceptance) was analysed using a survival analysis and log-rank test with tree nutritional quality class and beetle treatment group as factors, and a Cox's proportional hazards test, which included both of these factors and their interaction term. Distance travelled was rank-transformed and analysed using a two-factor ANOVA with a Tukey's Honest Significant Differences test.

All analyses were performed using the R Programming Language and Environment (v.2.14.0) (R Development Core Team, 2011).

RESULTS

Energetic condition upon emergence

Despite a statistically asymmetric response between male and female beetles, both groups showed a qualitatively similar emergence pattern. Beetle energetic condition was higher near the start of the emergence period, subsequently dropping off at the end of the emergence period (Table 2; Fig. 2a); however, there was substantial variation present. Most beetles emerged during the first half of the emergence period, with males and females both following a Weibull distribution ($\alpha_f = 1.724872$, $\beta_f = 9.674882$; $\alpha_m = 1.82726$, $\beta_m = 9.94895$) (Figs. 2d, e). CUBE profiles showing the probability of a beetle emerging on a particular day with a particular energetic condition are shown in Figs. 2b, c.

Host acceptance experiment

Our temperature treatments produced beetles in relatively poor and good energetic condition ($F_{1,211} = 4.81$, $P = 0.0294$; Fig. 3). Low-energy beetles (L) accepted trees of poor nutritional quality (P) sooner than did high-energy beetles (H), and beetles on trees of good nutritional quality (G) accepted them sooner than beetles on trees of poor nutritional quality (Fig. 4; log-rank: $\chi^2 = 84$, d.f. = 3, $P < 0.001$; Cox's proportional hazard: all $P < 0.01$ except the interaction term, which was non-significant). High-energy beetles travelled further than those with low energy on trees of poor nutritional quality (Fig. 5; Table 3).

DISCUSSION

This is the first study to use a manipulative experiment to test the effect of energy reserves on individual host selection decisions in bark beetles, and to characterize the variation in individual mountain pine beetles' timing of and energetic condition at emergence. Reduced choosiness as a result of a decline in individual state is a common theme in behavioural ecology, affecting a variety of behavioural decisions such as host selection (e.g. Roitberg *et al.*, 1992, 1993; Wajnberg *et al.*, 2006), foraging decisions (e.g. Nonacs, 2001), and mate selection (e.g. Hunt *et al.*,

Table 2. Cubic polynomial regression model for beetle somatic energy condition vs. date of emergence

	Estimate	S.E.	*t*-value	*P*-value
(*Intercept*)	−0.1697	0.0262	−6.47	<0.001
Day	0.0682	0.0081	8.39	<0.001
Day^2	−0.0056	0.0007	−8.02	<0.001
Day^3	0.0001	0.0000	6.01	<0.001

Note: $r^2_{adj} = 0.07892$; $F_{3,2049} = 59.61$; $P < 0.001$.

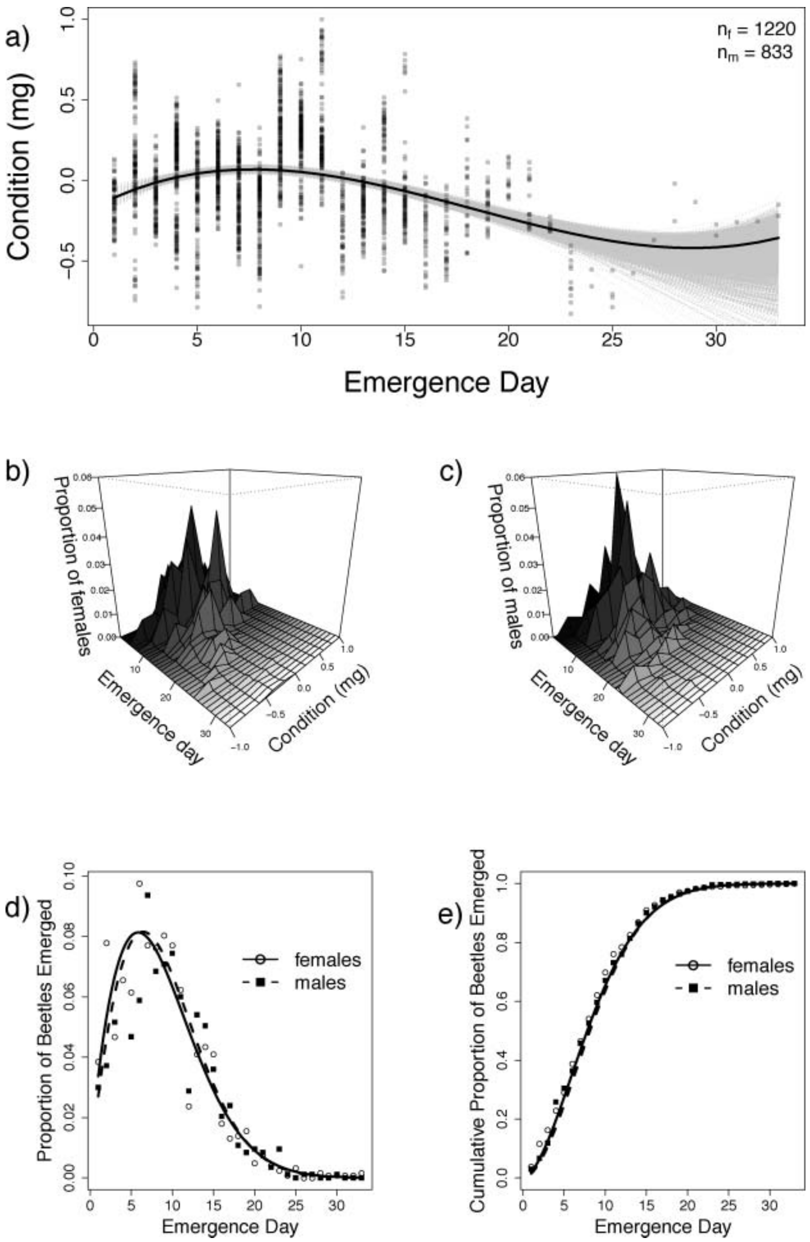

Fig. 2. Beetle energetic condition upon emergence (females, $n = 1220$; males, $n = 833$): (a) polynomial regression curve of date of emergence and energetic condition for both sexes (solid black) with bootstrapped regression curves (light grey) ($N = 10{,}000$); (b) proportion of female beetles with varying energetic condition emerging daily (female condition upon emergence profile); (c) proportion of male beetles with varying energetic condition emerging daily (male condition upon emergence profile); (d) proportion of female (open circles, solid line) and male (closed squares, dashed line) beetles emerging daily fit using a Weibull distribution ($\alpha_f = 1.724872$, $\beta_f = 9.674882$; $\alpha_m = 1.82726$, $\beta_m = 9.94895$); (e) cumulative proportion of female and male beetles emerging daily fit using a Weibull distribution [parameters as in (d)].

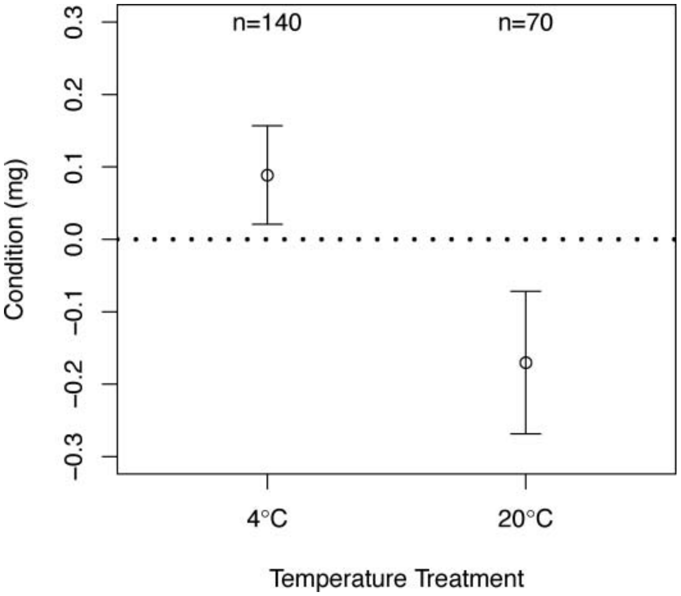

Fig. 3. Effect of low and ambient temperature treatments on mean beetle energetic condition. Error bars indicate standard errors.

Table 3. Two-factor ANOVA of vertical distance travelled before accepting host, for beetles with high or low energy reserves on hosts of good or poor quality

	Sums of squares	*F*-value	*P*-value
(*Intercept*)	68.36	8.8489	<0.001
Beetle energy reserves	0.48	0.0687	0.984
Tree quality	524.53	75.6429	<0.001
Beetle energy reserves × Tree quality	105.23	15.1751	<0.001

Note: $F_{3,136} = 33.01$; $P < 0.001$.

2005; Lynch *et al.*, 2005). The results of this study (Figs. 4 and 5) support the prediction that high-energy beetles are choosier (slower to enter) than low-energy beetles at selecting host trees, in a manner consistent with the condition-matching hypothesis. We did not observe a significant interaction between a beetle's energetic (i.e. somatic) condition and the nutritional quality of the host tree, suggesting that these independently influence beetles' decisions. Low-energy beetles accepted trees of poor nutritional quality sooner, and traversed the bark significantly less than did high-energy beetles. These results validate the basic predictions of previous work by Chubaty *et al.* (2009), who modelled the host selection decisions of mountain pine beetles using a dynamic state variable model that based individuals' decisions on distribution and nutritional quality of host trees, conspecific attack densities, the time left in the season to find a suitable host, and individuals' energy reserves. While previous work with mountain pine beetle host selection has suggested

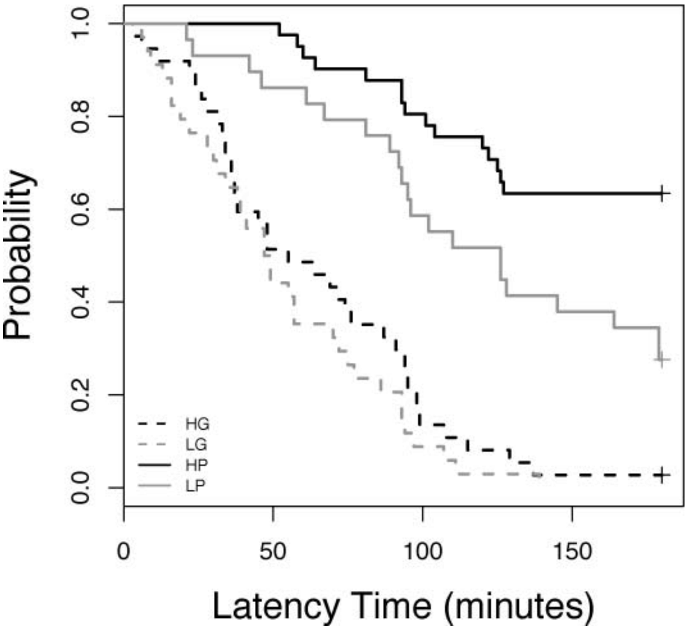

Fig. 4. Kaplan-Meier survival plots showing latency time on hosts of poor and good nutritional quality (time until acceptance) of beetles with high and low energy reserves. Steeper slopes indicate shorter delays accepting the host tree (i.e. beetles accept the tree more readily), whereas shallow slopes indicate longer delays before host acceptance. HG denotes high-energy beetles on trees of good nutritional quality; HP denotes high-energy beetles on trees of poor nutritional quality; LG denotes low-energy beetles on trees of good nutritional quality; and LP denotes low-energy beetles on trees of poor nutritional quality.

support for the safe-site hypothesis, the researchers could not exclude the condition-matching hypothesis (Latty and Reid, 2010). Our results do not support the safe-site hypothesis.

Our sample beetles used to generate CUBE profiles and our experimental beetles are from different populations; thus, their residual-derived energetic conditions cannot be compared directly (Jakob *et al.*, 1996). However, our temperature treatments produced groups of beetles representative of those emerging relatively early in the season, but with either high or low lipid reserves. Beetles in the ambient temperature treatment had much lower lipid reserves than beetles stored in the fridge. As a result, we saw much higher mortality in the ambient temperature treatment (as indicated by the difference in sample sizes between the two groups). These two beetle groups likely represent the extremes of the range of somatic energetic conditions found in host-seeking beetles, yet their behavioural differences demonstrated the flexibility of their host-selection strategies.

Animal dispersal and habitat selection models increasingly consider the role of individual variation and state-dependent decisions on behaviour, and their population-level outcomes. Models that account for individual variation/heterogeneity in behaviour make better predictions of resultant distributions at larger spatial scales than those that do not (e.g. Morales and Ellner, 2002). There are numerous examples of the importance of including individual behaviour when modelling populations, including the spread of invasive species and disease, and conservation (reviewed in Patterson *et al.*, 2008). Individual variation affects decisions in the

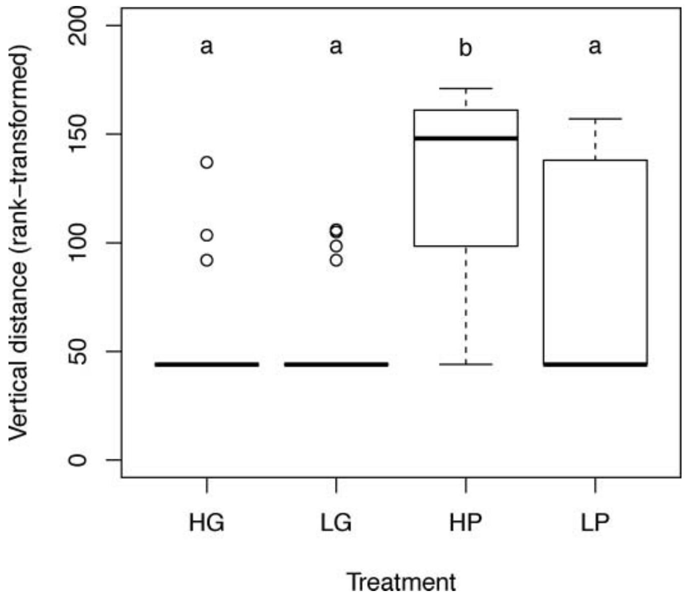

Fig. 5. Box-and-whisker plot showing vertical distance travelled before accepting host for beetles with high or low energy reserves on host trees of good or poor nutritional quality. Bold lines indicate the median; boxes denote the first and third interquartile range; whiskers indicate the data range within 1.5 times the interquartile range from the box; and open circles indicate data points outside the whisker range (i.e. outliers). Lower-case letters above each treatment's box highlight significant differences between treatments using an ANOVA with Tukey's Honest Significant Differences test. HG denotes high-energy beetles on trees of good nutritional quality; HP denotes high-energy beetles on trees of poor nutritional quality; LG denotes low-energy beetles on trees of good nutritional quality; and LP denotes low-energy beetles on trees of poor nutritional quality.

current generation, and may also carry over into future generations if such behaviours are heritable (e.g. Wallin *et al.*, 2002) or in the presence of maternal effects (e.g. Stamps, 2006). Additionally, research into consistent individual differences (i.e. behavioural syndromes) is exploring how decisions made in one dimension of behaviour (e.g. habitat selection) may correlate with decisions made in other dimensions of behaviour across an individual's lifetime (e.g. 'choosiness' in general, or in mate choice) (Sih *et al.*, 2004; Pruitt *et al.*, 2011). Thus, understanding the extent of individual variation in natural populations and the role it plays in animal decision-making is an essential first step in developing more accurate models of dispersal and habitat selection, and of behaviour more generally.

In our present study, we quantitatively characterized the variation in energetic condition at and timing of emergence for beetles of both sexes. As previously mentioned, although there were statistically significant differences between female and male beetles, they exhibited qualitatively similar emergence patterns. Beetles emerging earlier during the emergence period were in better energetic condition than those emerging near the end, and beetle emergence followed a Weibull distribution with most beetles emerging during the first half of the emergence period. These patterns can be summarized as condition upon beetle emergence (CUBE) profiles, which describe the probability of a beetle emerging on a particular day with a particular energetic condition. CUBE profiles summarize this relationship better than a polynomial regression due to the substantial variation present and the regression's subsequently low R^2 value. CUBE profiles are useful for parameterizing individual-based simulation models that incorporate beetle emergence. This work further enhances the development of mountain pine beetle host selection models to understand better beetle outbreak dynamics within and among forest stands. These models could be further expanded and developed to assess disturbance patterns at the landscape level.

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