Connections between individual dispersal behavior and the multi-scale distribution of a saproxylic beetle

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CONNECTIONS BETWEEN INDIVIDUAL DISPERsal
BEHAVIOR AND THE MULTI-SCALE DISTRIBUTION
OF A SAPROXYLIC BEETLE

A Dissertation
Submitted to the Graduate Faculty of the
Louisiana State University and
Agricultural and Mechanical College
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

in

The Department of Biological Sciences

by
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B.S., Brigham Young University, 2001
M.S., Brigham Young University, 2004
December 2010
For my parents Richard E and Twila Davis Bird,

and my parents-by-marriage, G. Lymon and Linda Keeler Jackson
Acknowledgments

This dissertation was accomplished with the help of a dynamite group of scientists at Louisiana State University. I would particularly like to thank my advisor, Jim Cronin, who let me work independently but provided prompt and in-depth feedback when I needed it. In addition, Jim provided an example of how a powerhouse work ethic can lead to high quality science.

I relied heavily on the camaraderie created by my fellow graduate students in the Cronin lab. Each one of them was willing to drop what they were doing and rescue a labmate in times of academic (or other) crisis. In addition to being an excellent scientific peer, Alyssa Hakes made fantastic vegan cupcakes and cheered me on when I most needed it. Forrest Dillemuth let me borrow his chainsaw, introduced me to GIS, and saved me countless times from taking myself too seriously. Amanda Accamando daily provided a listening ear and level-headed counsel on all things scientific and personal. Ganesh Bhattarai taught me crucial GIS skills and honed my philosophical and moral reasoning. Together my labmates greatly improved the quality of my public speaking with their valuable feedback.

Also in the Cronin lab were a number of talented and energetic undergraduates who contributed their time to this work including Farrar Brown, Erick Rietschier, Thomas Webb, Maria Waight, Chantal Miguel, Charlotte Gates, and Phuong-Anh Truong. I especially appreciate the contributions of Tristan Robert and Amanuel Zeccarias who made authorship-worthy contributions to chapters two and three, respectively.

I benefited from cooperation with two key collaborators, Kristen Baum and Kenny Rose. As a post-doc in the Cronin lab, Kristen introduced me to passalid beetles and has provided me with strong feedback and encouragement ever since. Kenny Rose generously invited me to his lab for five months, taught me Fortran, and provided me with expert advice on model design.
I appreciate the aid of my committee members. Meredith Blackwell provided valuable insight into the microbial symbionts of passalid beetles. Chris Carlson allowed me the use of his field equipment and enhanced my knowledge of insect taxonomy and evolution. Kyle Harms reliably offered key insights concerning experimental design and underlying theory. On numerous occasions, Richard Stevens allowed me to think out loud as he helped me develop my ideas. Derek Johnson started my education in ecological modeling and provided me with key criticisms on my dissertation.

The broader LSU community provided much-needed encouragement and intellectual support. The ecologists in the labs of Kyle Harms, Richard Stevens and Bill Platt and the entomologists in Chris Carlton’s lab created an atmosphere of scientific rigor and enthusiasm. From these labs, I appreciate the comments and friendship of Tim Paine, Jane Carlson, Heather Passmore, Paul Gagnon, Jonathan Myers and Raelene Crandall. Jonathan Myers in particular offered helpful comments on talks and was a fantastic co-instructor for a senior level ecology course. I benefitted greatly from the zest for ecology and evolution which emanates from the professors and graduate students of the Louisiana State University Museum of Natural Science. I relied on Verity Mathis in particular who generously volunteered the use of her home while I finished my dissertation.

I thank the many Louisiana residents and organizations who allowed me to conduct research on their property including Alligator Bayou, A. O. Wilberts & Sons, Joseph Barry, Irma & Alfred Fleming, Bobby Fulmer, Louisiana Fish & Wildlife, Louisiana State Parks, Louisiana State University, The Nature Conservancy, Carroll Olivier, Roy O. Martin Lumber, US Fish & Wildlife. Numerous individuals at these locations and elsewhere in Louisiana provided help during field work. I appreciate The Bicycle Shop and Capitol Cyclery for collecting used bicycle
tubes for my field work, Larry Dugas at Lake Fausse Pointe State Park for accompanying me on field work, Danny and Sharon Wiley at Larto Lake for their spontaneous donation of a paddle boat, Russell Burton Axtell Jr. and Russell Burton Axtell III for their help with perceptual range experiments, Hunter Roth for assistance in the wood shop, and arborist Glenn Wilson at the LSU Burden Center for the donation of decayed trees.

I have endless respect and love for my family whose contribution is immeasurable. I hope to emulate my father, Richard E. Bird, who, though now passed, inspired me with his keen intellect, his humble yet insatiable curiosity, his ability for hard work, and his unfailing respect for evidence. My wonderfully supportive mother, Twila Davis Bird, continues to model in her own work a passion for rigorous investigation and excellent writing. G. Lymon and Linda Keeler Jackson, my parents-by-marriage, are outstanding in their encouragement, and I particularly thank them for taking an inconvenient 1400 mile flight to move us out of our house when I was swamped with the last touches to my dissertation.

Most of all I thank my husband, Nathan Daniel Jackson, who has filled the roles of idea filter, editor, comic relief, sounding board, fan club leader, field worker, and daily companion. I would not have wanted to do this without him.
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Abstract

Species incidence results from a complex interaction among species traits (e.g., mobility and behavior), intra- and inter-specific interactions, quality and configuration of the landscape, and historical events. Determining which factors are most important to incidence is difficult because the multiple processes affecting incidence operate at different temporal and spatial scales. I conducted an empirically-based study relating individual behavior (dispersal, habitat selection, and intra-specific interactions) with hierarchically-organized environmental filters to predict the incidence of *Odontotaenius disjunctus* (Passalidae), a saproxylic (= decayed wood dependent) beetle common to eastern North American forests, at multiple spatial scales. In dispersal experiments, *O. disjunctus* movement was faster and more linear in suitable habitat than in unsuitable matrix (non-forest), and *O. disjunctus* exhibited a strong response to a high-contrast boundary between forest and open-field. A hierarchically-organized (log-section < log < subplot < forest plot) survey of incidence across 22 forest plots in Louisiana showed that patchiness in incidence was greatest at fine-scales (log-section and log), partly in relation to two environmental variables: decay state and log surface area. In fine-scale habitat selection experiments, resettlement distances were usually less than 5-10 meters, and immigration was positively influenced by log size and the presence of conspecifics, although aggregation associated with conspecific attraction did not occur because emigration balanced immigration. Additionally, population growth rate showed negative density dependence in post-settlement experiments. Finally, I developed an individual-based, spatially-explicit simulation model to relate fine-scale response to cues (habitat, mate, and conspecific density) and dispersal limitation to the density-area relationship. Unlike conspecific search, mate search did not result in large aggregations of individuals on large patches, but instead resulted in almost even density among
patches. Both habitat and mate search led to high overall incidence even when dispersal limitation was high. I conclude that *O. disjunctus* is a low-mobility species for which incidence is primarily determined by fine-scale interactions with conspecifics and the environment, and for whom high incidence can be explained in part by efficient use of cues during habitat search. Although sensitivity to large-scale habitat loss is a consistent pattern across taxa, this study emphasizes the overriding importance of fine-scale processes in predicting incidence.
Chapter 1: Introduction

The importance of an integrated theory of spatial ecology is apparent when I consider that many species live in a rapidly changing and spatially complex environment (Andren 1994, Fahrig 2003). Alterations to the bottomland hardwood forests of the southeastern United States provide an example of the extent to which the spatial context of species has been altered. In the Mississippi River Alluvial Valley, for example, more than 50% of the bottomland hardwood forest present in the 1930s was gone by the 1980s (Rudis and Birdsey 1986, McWilliams and Rosson 1990), most of it converted to agriculture (MacDonald et al. 1979). Furthermore, the hydrology of the area has been aggressively altered by over 5900 km of levees controlling the Mississippi River and its tributaries (IFMRC 1994). Changes in tree quality within forests may be as rapid as changes in the size of forests. Management for timber has resulted in a 21% and 46% decrease in coarse woody debris volume relative to public land in Georgia and South Carolina, respectively (McMinn and Hardt 1996). Management of biodiversity, therefore, will require an understanding of species’ response to an environment that is spatiotemporally dynamic at multiple scales.

A major obstacle to integrative studies of a species’ incidence across multiple scales is the fact that disciplines in ecology are largely confined to a single organizational level. Behavioral ecologists tend to focus at the fine-scales at which individuals acquire territories (Fretwell and Lucas 1969), select mates (Real 1990), and interact with conspecifics (Stamps 1988). Populations are the domain of population ecologists who tend to consider factors affecting birth and death rates such as resource quality (Rodenhouse et al. 1997), competition (Pianka 1970) and predation (Lotka 1925, Volterra 1926). Population ecologists may also study subdivided populations, in which case they may focus on the processes of extinction and
colonization (Levins 1969, Hanski 1994). At even broader spatial scales, landscape ecologists consider those factors that influence the patchy population as a whole, such as the effect of habitat abundance on overall incidence rates (With and King 1999, Fahrig 2001, 2002).

An understanding of the mechanisms underlying incidence at multiple scales will require a unification of these disciplines. Two recent areas of study are moving ecology toward this goal. The first area of study focuses on pattern and scale. The key idea in this area of study is that pattern (or variation) depends on the scale of observation, and that the scale(s) at which pattern is most apparent will imply something biologically significant about an organism (Levin 1992). The second area, called “the behavioral ecology of landscapes” (Lima and Zollner 1996), focuses attention on the landscape-level outcomes of the individual processes of dispersal and habitat selection. This field is characterized by interest in the importance of information acquired by individuals in determining movement behavior and subsequent distribution.

I combined these two approaches to yield powerful mechanism-based conclusions about the interaction between an organism and its landscape. Specifically, I used a combination of experiments, field surveys, and modeling to relate fine-scale movements and conspecific interactions to the multi-scaled incidence of a saproxylic (=decayed-wood dependent) beetle, *Odontotaenius disjunctus* Illiger (Coleoptera: Passalidae).

**STUDY SYSTEM**

*Odontotaenius disjunctus* is a large beetle (~32 mm) whose range covers eastern North America from Florida to southern Ontario, and from Kansas to the east coast (Schuster 1978). Socially monogamous *O. disjunctus* couples create extensive galleries in wood in which they care for their offspring into adulthood (Schuster and Schuster 1985), a process that takes about three months during the summer (in North Carolina, Gray 1946). During this time they are
seldom found outside of their log (Chapter 3), and presumably leave the log later only to find a new breeding territory. *O. disjunctus* is highly territorial (Gray 1946, Schuster 1975a) and avoids densities of greater than one pair per 28 dm$^2$ log surface area (Chapter 3). The process of mate and habitat location is not well-understood, but evidence suggests that one beetle, either male or female, initiates a gallery and is joined by a mate within a few days (Schuster 1975a). Flight is extremely rare (Hunter and Jump 1964, MacGown and MacGown 1996), but the vast majority of movements are cursorial (Chapter 2). Movement is especially slow in non-forest habitat and is generally avoided (beetles exhibit a strong reflection response to forest boundaries, Chapter 2). Average adult lifespan of *O. disjunctus* is unknown, but is probably between 2 and 5 years (Gray 1946, Schuster and Schuster 1997), which encompasses 2-5 breeding seasons.

**OVERVIEW OF CHAPTERS**

In this dissertation, I studied the ways in which dispersal, environmental filters, and behavioral response to habitat, mate, and conspecific cues combined to influence the incidence of *O. disjunctus*. The overriding theme connecting these studies is the outcome that incidence is not a simple result of dispersal, landscape, or behavior, but is instead the product of their interaction.

In Chapter 2, I investigated three important aspects of *O. disjunctus* dispersal biology: 1) its movement behavior (displacement, speed, linearity); 2) its response to the boundary between forest and open field; 3) seasonal and diurnal variation in movement activity. These dispersal data were an essential foundation to the following chapters, providing a mechanistic understanding of the scale and character of *O. disjunctus* interactions with the landscape.

For Chapter 3, I conducted a survey of *O. disjunctus* incidence across a broad range of spatial scales (log-sections to 3600 ha landscapes). I used this multi-scale analysis of incidence
to inform the development of scale-appropriate habitat selection experiments to determine the relative importance of mechanisms underlying incidence. Specifically, I quantified three processes that can influence dispersion of beetles: 1) use of habitat cue; 2) use of conspecific cues; and 3) settlement distance.

In Chapter 4, I investigated the population-level outcomes of fine-scale response to cues by building a biologically realistic spatially-explicit individual-based model of movement, reproduction, and mortality. For this study, I had two specific goals: 1) to evaluate the long-term population and landscape consequences of informed dispersal based on three different cues (habitat, mate, or conspecific density) with a particular emphasis on their contribution to the density-area relationship; and 2) to make predictions concerning the degree of cue-sensitivity expected under different levels of dispersal limitation.

I discuss the two major insights provided by this study in Chapter 5: 1) environmental filters and behaviors at fine-scales (e.g., within the neighborhood of individuals) may be most important to species incidence; and 2) low-mobility at fine-scales does not necessarily equate to high sensitivity to forest loss, but rather the effect of habitat loss on incidence will probably depend on the information animals use during dispersal.
Chapter 2 : Habitat-Specific Movement and Edge-Mediated Behavior of a Saproxylic Insect, *Odontotaenius disjunctus* (Coleoptera: Passalidae)¹

INTRODUCTION

Dispersal is a fundamental aspect of an organism’s life history, affecting population and community dynamics as well as local and regional persistence (MacArthur and Pianka 1966, Brown and Kodric-Brown 1977, Pulliam 1988, Hanski 1999). In relation to local and regional persistence, dispersal data are essential for 1) understanding the effects of habitat loss and fragmentation on population viability (Beissinger and Westphal 1998), 2) determining connectivity among habitat fragments (Fahrig and Merriam 1994), 3) constructing habitat management strategies to promote population persistence (Fahrig and Merriam 1994), and 4) developing and testing models of movement (Ovaskainen 2004) and spatial/temporal dynamics (Pulliam et al. 1992). Dispersal is particularly crucial for insects breeding in decaying wood (Ranius 2006), an ephemeral and patchily distributed resource.

As a result of extensive forest destruction and fragmentation, many forest-dwelling beetle populations are declining (Didham et al. 1998, Niemela 2001). For dead-wood dependent (saproxylic) insects, the quality and availability of resources within fragments are also greatly affected by forest management practices such as fuel extraction (Jonsell 2007) and selective or wholesale timber harvesting (Martikainen et al. 2000, Grove 2002, Muller et al. 2008). In Sweden, for example, 25% of saproxylic species (mostly beetles) are threatened or endangered largely because of forest loss and changes in the quantity and quality of coarse woody debris (Dahlberg and Stokland 2004 as cited in Jonsson et al., 2006).

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To date, data on dispersal of saproxylic insects are scarce and most available data concern members of the Scandinavian saproxylic beetle community and their emigration and colonization patterns within forests (Jonsell et al. 1999, Ranius and Hedin 2001, Jonsell et al. 2003, Jonsson 2003, Hedin et al. 2008). No data exist on the responses of these organisms to forest edges and non-forest (matrix) habitats.

I analyzed the movement of the saproxylic beetle, *O. disjunctus* Illiger, which relies on walking as its primary form of locomotion. *O. disjunctus* is a gallery-forming beetle commonly found in decaying hardwood in eastern North America. The objectives of this study were to 1) assess the terrestrial movement (e.g., displacement, speed, and linearity) of *O. disjunctus* as it traveled within the forest and within non-forested habitat, 2) observe the response of *O. disjunctus* when placed at the sharp boundary between forest and open field, and 3) describe the seasonal and diurnal dispersal patterns of *O. disjunctus*. In addition, because temporal patterns of passalid dispersal have not been reported (but see Schuster 1975a), I provide data concerning both seasonal and diurnal activity patterns as well as a description of the sex-ratio and age of dispersers throughout the year.

I tested several predictions about how *O. disjunctus* moves. First was the prediction that *O. disjunctus* would move faster and more linearly in non-forest than in forest habitats. This prediction is based on simulation experiments performed by Zollner and Lima (1999), in which the optimal path linearity was assessed for landscapes with different patch densities. These researchers found that optimal path linearity decreased slightly as resource density increased. Empirical studies generally have supported these results, with animals maximizing displacement in areas devoid of resources (Haynes and Cronin 2006, Schtickzelle et al. 2007).
I also tested the prediction that *O. disjunctus* movement is well-described by a correlated random walk – a common null model of animal movement (Turchin 1998) that fits the movement patterns of many animals (see Kareiva 1982). Deviation from the net displacement predicted by a correlated random walk model can signal non-random processes (e.g., attraction to a resource) or complex movement behavior (e.g., systematic search or autocorrelation in movement behavior).

The response of an organism to a habitat boundary can have large effects on its spatial population dynamics. Animals that are reluctant to cross habitat edges tend to have increased patch occupancy times, decreased emigration rates (Ovaskainen and Cornell 2003, Haynes and Cronin 2006), and are expected to make greater use of corridors (connecting strips of suitable habitat, Haddad 1999, Baum et al. 2004). Studies of butterflies and birds indicate that habitat specialists are more likely to avoid crossing a habitat edge than are generalists, especially when the contrast between habitats is high (Rail et al. 1997, Ries and Debinski 2001). I expected that as a forest specialist, *O. disjunctus* would avoid crossing into non-forested habitat when confronted with a high-contrast boundary.

**Study System**

*O. disjunctus* (commonly called the horned passalus) is one of the main gallery formers in decaying hardwood trees in the eastern United States (Ausmus 1977), with a range extending from Florida to southern Canada, from the Atlantic coast to eastern Kansas (Schuster 1978). *O. disjunctus* displays a preference for hardwood that has been dead for at least two years, particularly oak (Gray 1946). A lifespan of at least two years has been recorded in the wild (Gray 1946), however other passalid species in captivity have survived for more than four years (Schuster and Schuster 1985). *O. floridanus*, whose range is restricted to peninsular Florida, and
*O. disjunctus* are the only passalid species in eastern North America (Schuster 1994), although between 700 and 1000 passalid species exist worldwide (mostly tropical, Boucher 2005). Passalids are large beetles; *O. disjunctus* averages 3 cm in length.

Passalids present a high level of sociality, exhibiting both cooperative brood care and overlapping generations (Brandmayr 1992). Not only do both sexes provide parental care until adulthood is reached (> 3 months), but adult offspring help parents to maintain the pupal cases of their younger siblings (Schuster and Schuster 1985, Valenzuela-Gonzalez 1993). *O. disjunctus* creates long galleries lined with the digested wood on which larvae rely for food (Pearse et al. 1936) and from which offspring are likely to acquire wood-digesting gut microbes (Suh et al. 2003, Nardi et al. 2006). *O. disjunctus* larvae are abundant in galleries during June, July, and August (Gray 1946).

Passalids are assumed to leave a log only when in search of a mate or a new breeding territory. Passalidae tend to have reduced wings and limited geographical ranges, leading most researchers to conclude they have limited vagility (Schuster and Cano 2006). *Spasalus crenatus* MacLeay, the one passalid species for which dispersal data are available, shows a strong tendency to colonize logs within 6 m of its release point (Galindo-Cardona et al. 2007).

Although a few instances of flight in *O. disjunctus* have been reported (Hunter and Jump 1964, MacGown and MacGown 1996), the focus of this study was on walking behavior. During over 100 hours of direct observation of passalid beetles, I did not observe any flight. Furthermore, flight intercept traps deployed in the forest for six months (June – December 2004) failed to yield a single individual, even though five drift fences surrounding nearby decaying logs each yielded an average of 35 individuals during the same time period. Similarly, a flight-intercept trap run by Hunter and Jump (1964) yielded only one horned passalus in a four month
period. Schuster and Schuster (1997) noted that even passalids capable of flight will walk for long distances. Walking behavior is clearly the primary mode of movement for *O. disjunctus* and is therefore expected to make the greatest contribution to the beetle’s dispersal, especially at the local scale (i.e., among logs within a forest fragment).

**MATERIALS AND METHODS**

**Habitat-Specific Movement Behavior**

*O. disjunctus* adults were tracked following their release within forested habitat and open fields (urban lawn and cattle pasture) to determine if movement behavior differed among habitat types. Using a hatchet to carefully dissect galleries, I extracted beetles from hardwood logs during the summers of 2004 and 2006. Logs were located at Louisiana State University (LSU) Burden Research Plantation (Burden; 30°24’N 91°06’W WGS84) and LSU’s Central Research Station (CRS; 30°23’N, 91°11’W WGS84). Beetles were held under controlled laboratory conditions with unlimited access to food (field collected decaying wood) for less than two days prior to tracking, and those that showed signs of physical injury (usually broken or missing legs) were not used. Each beetle was used only once.

Releases in forested habitat were conducted at Burden Research Plantation. Beetles were released at least 10 m from the nearest log, a distance much greater than the perceptual range suggested by preliminary trials (~ 1 m, H.B.J., unpublished data). The cattle pasture was a single field located at CRS. During preliminary trials, beetles would not move in open fields under full sunlight, but instead remained immobile beneath vegetation. Therefore, all open field and boundary trials (below) were conducted during twilight (0600-0700 CDST or 1900-2000 CDST). Grass culms averaged 7.9 cm (± 0.3 se, n = 19 – 1 dm^2 quadrats) in height with a density of 3.2 culms/dm^2 (± 0.2). The urban lawn was located at LSU (30°24’N, 91°10’W WGS84) and had
culm heights that were significantly shorter (5.5 ± 0.3 cm, n = 31 – 1 dm² quadrats; t₄₇ = -2.76, P = 0.008) and culm densities that were no different (4.1 ± 0.3 culms/dm²; t₄₇ = 1.49, P = 0.143) than in the pasture. Release points in the forest or open fields were > 30 m from the edge.

O. disjunctus beetles were released one at a time by laying a collection cup containing one beetle on the ground and allowing it to leave on its own. Surveyor flags were used to mark the location of each beetle at one minute intervals (Turchin et al. 1991, Cronin et al. 2001). Beetle dispersal did not appear to be influenced by observer location; when an observer was in the path of a beetle, the beetle would simply climb over the observer’s foot and continue on; direction of movement did not change in response to observer position (H.B.J., unpublished data). A trial was terminated when a beetle stopped moving for more than five minutes or after 30 minutes had elapsed. During preliminary observations I found beetles that stopped movement for five minutes were unlikely to move within the next two hours. Using a triangulation program written in R 2.7.2 (available upon request from H.B.J.), the x-y coordinates of the flags were calculated, along with step length (distance between each successive flag), turning angle (relative change in direction), path length (total distance traveled), and net displacement (straight line distance from starting point) (Turchin et al. 1991, Turchin 1998). Movement paths were recorded for 25 beetles in the forest, 21 in the lawn, and 20 in the pasture. Hourly weather measurements recorded at CRS concurrent with beetle movements were downloaded from the LSU website (www.lsuagcenter.com). Although most beetles were extracted from logs, the tracks of an additional eight beetles caught in pitfall traps or found walking (n=10) were also observed in the forest so that the paths of naturally dispersing beetles could be compared with those of experimental beetles (i.e., those extracted from galleries, n=66).
I tested the hypothesis that movements are faster and more linear in open fields than in forest using a multivariate regression model (Krzanowski 2000) which included the dependent variables displacement rate (net displacement divided by time), velocity (path length divided by time), and net-to-gross displacement ratio. The latter quantifies the linearity of paths and is equal to net displacement divided by path length (Wilson and Greaves 1979); a displacement ratio of 1 is a straight line and 0 indicates a return to origin. Models with four sets of independent variables were compared: habitat alone, capture method alone (naturally dispersing versus gallery-collected beetles), both habitat and capture method, and neither. Displacement rate was square root transformed, velocity was log-transformed, and displacement ratio was logit transformed. All transformations were done to achieve the assumption of normality. I included air temperature and relative humidity as covariates in my analyses. Because intermediate temperatures are usually optimal for maximum velocity (Harrison and Roberts 2000), a quadratic term for air temperature was also included.

Model selection was based on information theory as described by Burnham and Anderson (Burnham and Anderson 2002). Akaike’s Information Criterion for small sample sizes (AICc) was used to select the best model or the best set of models. The model with the smallest AICc value was considered the best model. Models with AICc no more than 7 points greater than the lowest AICc were included in the “best set” because they are still considered informative (Burnham and Anderson 2004). After the best model was selected, the relative importance of each predictor variable in the final model was evaluated by partitioning the variance using the package “relaimpo” (Grömping 2006). This procedure is less sensitive to collinearity among predictor variables because it calculates the average change in explained variance associated with
the removal of an independent variable from a set of models. The set of models includes every possible combination of predictor variables (Lindeman et al. 1980).

Using subsets of these data for which beetle sex and length data were available (n = 58 and 28, respectively), I assessed whether sex or size predicted movement. The model selection process was identical to that described above.

I determined the proportion of beetle paths that fit the predictions of a correlated random walk model that was developed following the bootstrapping procedure described by Turchin (1998). A correlated random walk predicts net displacement of an organism based on the assumptions that step lengths and turning angles are random. A brief description of the bootstrapping procedure is as follows. A beetle’s step lengths and turning angles were randomly drawn with replacement from its empirical distributions to create a track equal in length to the original track, and the net squared displacement at each time step was calculated. One thousand tracks for each beetle were simulated in this manner. A beetle whose net displacement at any time was lower or greater than 99% of the simulated tracks (increased from 95% to adjust for inflated Type 1 error rates associated with multiple tests) is scored as a rejection (i.e., not fitting a correlated random walk). In order to predict whether a beetle’s net displacement tended to be lower than, equal to, or greater than predicted by a correlated random walk, an ordered logistic regression model was developed. Logistic regression models have a bivariate response (e.g., yes/no), while ordered logistic regression allows for an ordered multi-level response (e.g., less than, equal to, greater than) (Venables and Ripley 2002). Given the need for larger samples when using logistic regression, only those independent variables for which large samples were available were used (i.e., habitat and weather). Because I had no a priori reason to believe that weather would influence the probability of following a correlated random walk, the information
value of both habitat and weather variables was tested using the model selection method described above.

**Edge Behavior**

Beetles were released at random locations along a 300 m boundary between forest and pasture at CRS to assess their movement response to a high-contrast edge (n = 20). All trials were conducted at twilight (ten individuals in the morning and ten individuals in the evening) when direct sunlight was not a factor. The propensity of a beetle to emigrate from a forest was inferred from the direction of movement after being placed on the forest/pasture boundary. Path direction was calculated as the angle between the starting point and the final location of the beetle after up to 30 minutes of movement. Dividing the possible directions into thirds, each beetle’s path was assigned to one of three categories (towards the forest, on the boundary, and towards the pasture, Haynes and Cronin 2006). The null hypothesis that paths were equally likely to end up in one of these three directions was tested using Fisher’s Exact Test.

**Seasonal and Diurnal Dispersal Patterns**

Beetles were trapped while emigrating from or moving toward focal logs over 17 months (June 2004-October 2005). Five drift fences made of 30 cm tall aluminum flashing were placed around five large, moderately decayed logs, each containing at least one active colony of *O. disjunctus*. The presence of a colony was inferred when coarse sawdust distinctive of *O. disjunctus* activity was noted at the base of a log. Flashing was inserted at least 10 cm into the ground and 0.5 m from the log. Eight pitfall traps (375 ml cups) were spaced equal distances apart along each of the five drift fences with four on the inside (to capture emigrants) and four on the outside (to capture dispersing beetles from the broader forest community). Each trap was located under a small shelter to protect it from sun and rain. Traps were checked twice a week.
Five additional fenced logs were included in the survey from January 2005 through October 2005. All drift fences were located at Burden.

To evaluate diurnal patterns of activity, pitfall traps were checked twice daily (0800 and 1700 CDST) from 1 June 2005 – 23 June 2005. Due to a slowdown in dispersal activity at the end of June, twice daily trap-checks were discontinued until September, and then from 12 September 2005 – 17 September 2005.

Sex was determined postmortem (Schuster 1975b). Age was classified as either partial sclerotization (exoskeleton still had red highlights) or full sclerotization (exoskeleton completely black). Complete sclerotization typically takes eight to ten weeks following adult eclosion (Schuster and Schuster 1997). Length was measured from horn tip to abdomen apex using calipers, as described in Gray (1946).

Logistic regression was used to predict weekly dispersal activity. The response was the proportion of fences at which dispersers were caught each week. All combinations of the following independent variables were considered during model selection: minimum weekly temperature, minimum weekly relative humidity, mean weekly day length, and time since the beginning of the experiment. Day length data were gathered from the U.S. Naval Observatory website (www.usno.navy.mil). Time (i.e., number of weeks since the beginning of the study) was included to investigate the possibility of overall trends during the experiment. Quadratic functions of all weather variables were also considered in model selection.

The null hypothesis that the ratio of females to males was constant across months was evaluated using Fisher’s Exact Test for Independence (a test appropriate for tables of counts with low values, Fisher 1970). Tests were conducted separately for each fenced log, and the p-value was obtained with a permutation test (Ramsey and Schafer 2002). Bonferroni corrections for
multiple tests were applied (Ramsey and Schafer 2002). As a measure of disperser maturity, seasonal patterns in cuticle sclerotization were also analyzed using Fisher’s Exact Test for each fenced log.

The null hypothesis that dispersal during the day and night was equally likely was assessed using Fisher’s Exact Test. Because fewer hours were available to dispersers during daytime sampling (0800-1700 CDST), the null probability that dispersal would occur during the day was adjusted accordingly (9 hours daylight out of 24 h).

All analyses were conducted in R (R Development Core Team 2010). All reported intervals are 95% confidence intervals.

RESULTS

Habitat-Specific Movement Behavior

Displacement rate, velocity, and linearity were greater in the forest than in open fields (forest > lawn > pasture; Figure 2.1). Habitat, a highly informative predictor of movement behavior, was present in the best set of models for all three sample sets (Table 2.1). The best model predicting movement behavior included habitat, capture method, temperature, and relative humidity (Table 2.1). Displacement rate averaged 1.9 and 2.9 times faster, velocity averaged 1.6 and 2.7 times faster, and displacement ratio averaged 1.1 and 1.5 times more linear in the forest than in the lawn and pasture, respectively, after accounting for the effects of weather conditions (Table 2.2, Figure 2.1). Movement behaviors were more different between the two matrix habitats than between either matrix habitat and the forest. Differences were 27%, 36%, and 18% greater between lawn and pasture than between forest and lawn for displacement rate, velocity, and linearity, respectively (Table 2.2, Figure 2.1).
The fastest beetles were those that had been collected in pitfall traps prior to their release (i.e., the natural dispersers, n=10). Their displacement rate averaged 74% greater and their velocity averaged 1.5 times faster than log-collected beetles in the forest (Table 2.1, Table 2.2). The difference in linearity between pitfall- and log-collected beetles, however, was negligible (CI = -43% to +393% difference). The information value of capture method for explaining
movement was limited: the evidence value \((w_i)\) for a model excluding the effect of capture method was reasonably high (0.32, Table 2.1) and temperature and habitat explained 4-5 times more model variance (Table 2.3). Temperature and relative humidity were both positively related to movement rate and linearity (Table 2.2), although relative humidity explained only \(\frac{1}{4}\) the model variance of either temperature or habitat (Table 2.3). Temperature and habitat tended to explain equivalent proportions of the variation in movement variables (Table 2.3). The best models for predicting displacement rate and velocity had \(r^2\) values that exceeded 70% (Table 2.3), but the best models predicting displacement ratio had \(r^2\) values under 40%.

### Table 2.1 Summary of candidate models used to estimate movement behavior (displacement rate, velocity, net-to-gross displacement ratio), the probability of following a correlated random walk, and the probability of dispersal each week.

<table>
<thead>
<tr>
<th>Response</th>
<th>Sample size</th>
<th>Model</th>
<th>k</th>
<th>(\Delta AIC_c)</th>
<th>(w_i)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Movement Behavior</td>
<td>a) (n = 76)</td>
<td>habitat + capture method + T + T^2 + RH</td>
<td>8</td>
<td>0.00</td>
<td>0.68</td>
</tr>
<tr>
<td></td>
<td></td>
<td>habitat + T + T^2 + RH</td>
<td>7</td>
<td>1.53</td>
<td>0.32</td>
</tr>
<tr>
<td></td>
<td>b) (n = 58)</td>
<td>habitat + sex + T + T^2 + RH</td>
<td>8</td>
<td>0.00</td>
<td>0.99</td>
</tr>
<tr>
<td></td>
<td>c) (n = 28)</td>
<td>habitat + T + T^2 + RH</td>
<td>6</td>
<td>0.00</td>
<td>0.74</td>
</tr>
<tr>
<td></td>
<td></td>
<td>habitat + length + T + T^2 + RH + length</td>
<td>7</td>
<td>2.96</td>
<td>0.17</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T + T^2 + RH</td>
<td>5</td>
<td>4.53</td>
<td>0.08</td>
</tr>
<tr>
<td>2) Correlated Random Walk</td>
<td>(n = 76)</td>
<td>habitat</td>
<td>4</td>
<td>0.00</td>
<td>0.61</td>
</tr>
<tr>
<td></td>
<td></td>
<td>habitat + RH</td>
<td>5</td>
<td>2.28</td>
<td>0.19</td>
</tr>
<tr>
<td></td>
<td></td>
<td>habitat + T + T^2</td>
<td>6</td>
<td>4.41</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T + T^2</td>
<td>4</td>
<td>4.46</td>
<td>0.07</td>
</tr>
<tr>
<td></td>
<td></td>
<td>T + T^2 + RH</td>
<td>5</td>
<td>6.68</td>
<td>0.02</td>
</tr>
<tr>
<td></td>
<td></td>
<td>habitat + T + T^2 + RH</td>
<td>7</td>
<td>6.83</td>
<td>0.02</td>
</tr>
<tr>
<td>3) Dispersal Activity</td>
<td>(n = 72)</td>
<td>t + T + T^2 + DL + DL^2</td>
<td>6</td>
<td>0</td>
<td>0.59</td>
</tr>
<tr>
<td></td>
<td></td>
<td>t + T + T^2 + DL + DL^2 + RH</td>
<td>7</td>
<td>0.76</td>
<td>0.41</td>
</tr>
</tbody>
</table>

\(k\) = the number of estimated model parameters, \(\Delta AIC_c\) = the difference in AIC\(_c\) scores relative to the model with the lowest AIC\(_c\), \(w_i\) = Akaike weight indicating the evidence value for each candidate model, \(T\) = air temperature, \(RH\) = relative humidity, \(t\) = weeks since the beginning of the experiment, \(DL\) = average hours of day light per week. Only those models for which \(\Delta AIC_c\) was less than 7 are shown. Minimum weekly relative humidity was considered in models of dispersal activity but was not included in the most informative models shown here. See methods for details.
The sexes differed only in their path linearity and then only slightly. A male beetle was almost twice as likely (CI = 1.02 – 3.58) to follow a perfectly linear path than a female.

Temperature and habitat were 3 times more important when predicting path linearity (Table 2.3). Sex was of negligible importance when predicting displacement rate and velocity (Table 2.3).

There was little evidence that beetle size affected movement. When length was included in the model, it explained <1% of the variance in each measure of movement. Beetle length was not included in the best model predicting movement behavior (Table 2.1), but the model

### Table 2.2 Movement behavior in response to habitat type and capture method and change in weather conditions.

<table>
<thead>
<tr>
<th>Independent variables</th>
<th>Displacement rate (cm/min)</th>
<th>Velocity (cm/min)</th>
<th>Net-to-gross displacement ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>95 CI</td>
<td>95 CI</td>
<td></td>
</tr>
<tr>
<td></td>
<td>average</td>
<td>lower</td>
<td>upper</td>
</tr>
<tr>
<td>1) Response to habitat and capture method</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>log-captured</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>forest</td>
<td>20.84</td>
<td>13.01</td>
<td>30.50</td>
</tr>
<tr>
<td>lawn</td>
<td>15.31</td>
<td>6.73</td>
<td>27.36</td>
</tr>
<tr>
<td>pasture</td>
<td>8.84</td>
<td>3.21</td>
<td>17.25</td>
</tr>
<tr>
<td>pitfall-trap captured</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>forest</td>
<td>36.28</td>
<td>24.40</td>
<td>50.51</td>
</tr>
</tbody>
</table>

| 2) Impact of a 1 unit increase in weather conditions | | | | | | | | |
| T (°C) | 0.19 | 0.07 | 0.36 | 1.21 | 1.14 | 1.28 | 1.17 | 1.01 | 1.36 |
| T² (°C²) | 0.00 | 0.00 | 0.00 | 0.99 | 0.99 | 1.00 | 0.98 | 0.96 | 1.00 |
| RH (%) | 0.00 | 0.00 | 0.01 | 1.02 | 1.01 | 1.03 | 1.01 | 0.99 | 1.04 |

1) Average movement behavior of beetles under average weather conditions (28°C and 63% relative humidity). 2) The average change in each movement behavior associated with a one unit change in the weather condition of interest. Each movement behavior underwent a different data transformation, and these back-transformed values for weather conditions must be interpreted differently. For displacement rate, these values indicate the additive increase in movement behavior. For velocity, these values indicate the multiplicative increase in velocity (e.g., 1.18 times faster). For displacement ratio, these values indicate the multiplicative increase in the odds of a perfectly straight path (e.g., 1.14 times more likely). T = air temperature, RH = relative humidity.

The sexes differed only in their path linearity and then only slightly. A male beetle was almost twice as likely (CI = 1.02 – 3.58) to follow a perfectly linear path than a female.

Temperature and habitat were 3 times more important when predicting path linearity (Table 2.3). Sex was of negligible importance when predicting displacement rate and velocity (Table 2.3).

There was little evidence that beetle size affected movement. When length was included in the model, it explained <1% of the variance in each measure of movement. Beetle length was not included in the best model predicting movement behavior (Table 2.1), but the model
The majority of beetle paths were poorly predicted by a correlated random walk. Habitat was the only predictor included in the best model predicting violations of the correlated random walk model (Table 2.1). Fifty-one percent of beetles moving in the forest displaced further than expected by a correlated random walk model (Figure 2.2). In contrast, beetles in lawn and pasture tended to displace 83% and 78% less than expected, respectively (Figure 2.2).

### Table 2.3 Proportion of variance explained by each independent variable in the two best models predicting movement behavior (see Table 2.1).

<table>
<thead>
<tr>
<th>Sample set</th>
<th>Independent variables</th>
<th>Displacement rate</th>
<th>Velocity</th>
<th>Net-to-gross displacement ratio</th>
</tr>
</thead>
<tbody>
<tr>
<td>1) Best model: habitat + capture method + T + T^2 + RH (n=76)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>T*</td>
<td>28.6%</td>
<td>31.6%</td>
<td>15.6%</td>
</tr>
<tr>
<td></td>
<td>habitat</td>
<td>28.0%</td>
<td>31.4%</td>
<td>12.7%</td>
</tr>
<tr>
<td></td>
<td>capture method</td>
<td>6.7%</td>
<td>4.6%</td>
<td>2.7%</td>
</tr>
<tr>
<td></td>
<td>RH</td>
<td>6.7%</td>
<td>7.2%</td>
<td>3.1%</td>
</tr>
<tr>
<td></td>
<td>total % variance explained ( (r^2) )</td>
<td>70.0%</td>
<td>74.8%</td>
<td>34.1%</td>
</tr>
<tr>
<td>2) Best model: habitat + sex + T + T^2 + RH (n=58)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>T*</td>
<td>32.3%</td>
<td>33.8%</td>
<td>15.4%</td>
</tr>
<tr>
<td></td>
<td>habitat</td>
<td>31.3%</td>
<td>35.3%</td>
<td>15.5%</td>
</tr>
<tr>
<td></td>
<td>sex</td>
<td>0.3%</td>
<td>0.2%</td>
<td>4.3%</td>
</tr>
<tr>
<td></td>
<td>RH</td>
<td>6.6%</td>
<td>6.8%</td>
<td>2.8%</td>
</tr>
<tr>
<td></td>
<td>total % variance explained ( (r^2) )</td>
<td>70.5%</td>
<td>76.1%</td>
<td>37.9%</td>
</tr>
</tbody>
</table>

*These values indicate the combined importance of temperature and its quadratic term.

| habitat: habitat where beetle movements were observed. capture method: whether extracted from log or pitfall trap; T: air temperature; RH: relative humidity; Relative importance is measured as the average proportion of variance explained by each variable (sensu Lindemann, Merenda and Gold 1980). Relative importance for each independent variable sums to the total variance explained \( (r^2) \). Including length may have had some information value \( (\Delta \text{AIC}_c = 2.96); \) a model with \( 2 < \Delta \text{AIC}_c < 7 \) has some information value according to Burnham and Anderson, 2004).
Figure 2.2 Probability that a beetle’s net squared displacement is lower, equal to, or greater than the predictions of an empirically-based, beetle-specific correlated random walk (see Methods for description). Error bars are 95% confidence intervals.

**Edge Behavior**

When released at the boundary between forest and pasture, beetles were 14 times more likely to move into the forest than into the open field ($P = 0.027$). Seventy percent of beetles (CI = 46 – 88%) moved into the forest, while only 5% (CI = 0 – 25%) moved towards the pasture. The remaining 25% of the beetles remained at the forest-pasture boundary.

**Seasonal and Diurnal Dispersal Patterns**

Dispersing beetles were most abundant during spring and fall. The best model explaining weekly dispersal activity indicated that the odds of one or more dispersers being captured at a fence increased with intermediate temperature (CI = 29 - 207%/°C; quadratic CI = -0.2 – -2%/°C^2) and intermediate day length (CI = 22 – 51%/MJ*m^-2; quadratic CI = -0.001 – 0.002%/MJ^2*m^-4), and decreased with time since the observations began (CI = -2 – 4%/week; McFadden’s $\rho = 56.6\%$, Tables 2.1-2.3; Figure 2.3). The second best model explaining weekly dispersal activity included relative humidity (Tables 2.1-2.3) and indicated a slightly negative correlation between relative humidity and odds of dispersal (-4.1 – +0.02%/°% humidity).
Figure 2.3 Patterns of dispersal activity of *O. disjunctus* by week. Dispersal data represent the proportion of trial logs (2004 n = 5, 2005 n = 10) from which one or more beetles were caught each week.

Overall, incompletely sclerotized beetles comprised 28% ± 5% SE of dispersers. Fifty-nine percent (± 6% SE) of dispersers were female, a percentage not significantly different from the sex ratio within nearby logs (60%, *P* = 0.992). The proportion of dispersers that were recently eclosed adults and/or female remained constant throughout the study period (*P* > 0.05 for all drift fences), except in one outlier fence that had greater numbers of incompletely sclerotized beetles than usual in October 2004 (*P* < 0.001).

*O. disjunctus* beetles were 3.5 (CI = 0.91 – 14.51) times more likely to disperse during the day than during night or twilight (*P* = 0.04). Of 24 beetles caught during day/night trials, 15 were caught during the day. Overall, both seasonal and diurnal dispersal patterns suggest that more beetles move during warm weather.

**DISCUSSION**

The faster and more linear movements of *O. disjunctus* in suitable versus matrix habitat is the opposite of what was predicted by theory (Zollner and Lima 1999; see also Introduction) and empirical findings for a *Prokelisia* planthopper (Haynes and Cronin 2006), a flightless tansy leaf
beetle (*Chrysolina graminis*, Chapman et al. 2007), and the bog fritillary butterfly (*Proclossiana eunomia*, Schtickzelle et al. 2007). Slower movements in unsuitable habitat can be adaptive, such as when pausing increases resource detection or predator vigilance (Zollner and Lima 2005). Indeed, beetles paused frequently to stand on the tops of grass blades and leaf litter with raised heads and active antennae, indicating that attempts to search the environment may be a reason for slowed movement. Because *O. disjunctus* movement is probably restricted to natal and breeding dispersal events among logs (rather than foraging), movements which maximize displacement in the forest may indicate an effort to avoid kin competition or inbreeding by increasing distance from the natal site (Greenwood and Harvey 1982, Long et al. 2008). Furthermore, although beetles were released at distances from logs that were beyond their presumed perceptual range, the possibility that logs or their inhabitants influenced beetle movement in the forest should not be ruled out. On the other hand, faster movement in matrix may be optimal but animals may be unable to maintain optimal movement due to microclimatic (e.g., too much or too little sunlight, Ross et al. 2005) or structural (e.g., heavier ground cover, Schooley and Wiens 2004, Stevens et al. 2004) impediments. Furthermore, anthropogenically-driven changes may be too fast for populations to evolve optimal movement behaviors in all habitats (Fahrig 2007, Reeve et al. 2008b). Experiments in which ground cover, light, and surrounding cues (e.g., trees) were tightly controlled could illuminate the reasons for differences in movement between forest and field. Regardless of the reasons, it is clear that under natural conditions *O. disjunctus* alters its movement in different environments. This is the first study to quantify movement of a saproxylic beetle among different habitats, and adds to a growing list of studies indicating that animals modify their dispersal behavior in different habitat types (e.g. Conradt et al. 2000, Jonsen and Taylor 2000, Cronin 2003a, Haynes et al. 2007).
The occurrence of habitat-specific variation in movement behavior is important to consider when developing models predicting spatial spread (Tischendorf 1997, Ovaskainen 2004). For example, an *O. disjunctus* dispersal event of typical duration (35 min in this study) is expected to result in biologically significant differences in spatial spread among habitats (7, 5, and 3 m in forest, lawn, and pasture, respectively, after 35 min). Naturally dispersing beetles would achieve even greater net displacement (13 m after 35 min), indicating the importance of quantifying the differences between the movements of experimental subjects typically used in these types of studies and those made by natural dispersers. The short dispersal distances predicted by these data are supported by a trial in which 72 beetles were released and recaptured in logs a week later. This trial indicated an average colonization distance of 11.6 m (CI = 9.4 – 14.3 m, H.B.J, unpublished data). These results also emphasize the dispersal limitation these beetles experience; changes in inter-log or inter-forest distance that lead to isolation much greater than 15 m could impact the ability of *O. disjunctus* to successfully colonize a new log.

Similar dispersal challenges are expected for other saproxylic insects. Compared to other resources used by insects, decaying wood is relatively stable; coarse woody debris in Louisiana bottomland hardwood forests exhibit a half-life of 9 to 14 years after tree death depending on ground contact (Rice et al. 1997). Woody material in colder or drier habitats is expected to decay even more slowly, with half-life estimates of over 100 years for some tree species (Harmon et al. 1986). Theory predicts that animals associated with a stable resource have lower dispersal ability than animals associated with ephemeral habitats (Southwood 1962, Roff 1990, Denno et al. 1991). For this reason it is probable that other saproxylic insects are similarly dispersal limited and in many cases sensitive to anthropogenic impacts on forest health (e.g., Ranius and Hedin 2001). Assessments of saproxylic insect diversity should therefore include methods designed to
capture non-flying insects (e.g., eclector or pitfall traps, Ranius and Jansson 2002, Alinvi et al. 2007) in addition to more traditional methods targeting flying insects. My data suggest that non-dispersing individuals can be expected to have lower velocity and net displacement than natural dispersers. This is an important point because dispersal studies often rely on non-dispersing individuals (Galindo-Cardona et al. 2007) or individuals engaged in daily movement as opposed to dispersive movement (reviewed in Van Dyck and Baguette 2005), probably because sample sizes provided by individuals caught in the act of dispersal are inadequate (as with my system) or such individuals are difficult to distinguish from those engaged in routine movements. Even so, the movement of naturally dispersing beetles in my experiment was comparable to that of experimental beetles in shape if not in scale: capture method was not an important predictor of linearity. I expect the data collected from non-dispersing individuals to provide good information on the expected linearity of movement and relative differences in movement rate, but data from natural dispersers is necessary to estimate absolute velocity and net displacement for *O. disjunctus* and likely other animals.

Although the correlated random walk model is a good predictor of net displacement for other ground-moving beetles (e.g., some carabid beetles, Wallin and Ekbom 1994), it was inadequate for more than half of the individuals observed in this study. This prediction failure was due in part to significant autocorrelation (temporal lack of independence) in step lengths and turning angles (H.B.J., unpublished data) – violations of the assumptions of a correlated random walk. Turchin (1998) suggests that autocorrelation can result when steps are measured on a scale smaller than is meaningful to the organism. However, I were unable to remove autocorrelation by increasing the time interval over which movement behavior was measured (Turchin 1998). When autocorrelation in movement behaviors was incorporated into a modified correlated
random walk model, no significant differences between predictions and observations were found (H.B.J., unpublished data).

As with other specialist organisms (Rail et al. 1997, Ries and Debinski 2001, Stevens et al. 2006), *O. disjunctus* exhibits a strong response to a high-contrast boundary. A model incorporating edge-mediated behavior predicts that a strong bias towards suitable habitat will result in greater occupancy time and decreased emigration rates (Ovaskainen 2004), outcomes that may be optimal for organisms living in fragmented habitat. On the other hand, strong reluctance to leave suitable habitat can decrease colonization and increase extinction of isolated patches (Brown and Kodric-Brown 1977). The fact that *O. disjunctus* is common and widely distributed among forest fragments in the southeastern United States suggests that infrequent flight and/or rare inter-forest walking is effective at maintaining colonization rates (e.g., Jonsell et al. 2003), or within-forest dynamics are robust to local extinction. Whether walking or flying is the primary method for long-distance dispersal for *O. disjunctus* (as is the case for wild *Triatoma infestans* Klug (Hemiptera: Reduviidae), another insect capable of both flight and terrestrial movement, Richer et al. 2007) is a question best suited for indirect methods of investigation such as simulation experiments or population genetic studies.

The circannual patterns in *O. disjunctus* dispersal (spring and fall peaks) are roughly congruent with those found in Florida (Schuster 1975a). Although complete data on dispersal activity of other gallery-forming insects of coarse woody debris are not available, most disperse during the spring (carpenter ants: Sanders 1972, termites: Matsuura et al. 2007), or spring and fall (conifer-associated cerambycid beetles, Dodds and Ross 2002). Seasonal dispersal activity of temperate ground-moving beetles has been associated with temperature, humidity, resource availability, interspecific competition, and breeding activity (see Werner and Raffa 2003 for a
Breeding activity is an untested but likely reason for limited *O. disjunctus* dispersal during summer months. Larvae are most abundant during summer months (Gray 1946) and require the attention of both parents (Schuster and Schuster 1985).

The finding that the sex-ratio of *O. disjunctus* dispersers was equal to the sex-ratio observed in logs is consistent with theory suggesting that both sexes in monogamous mating systems would likely display equal dispersal tendencies, especially when responsibility for resource defense is shared by both partners (Greenwood, 1980, Greenwood and Harvey; see also Schuster and Schuster, 1985 and Schuster 1983). Similar to many bird species, *O. disjunctus* is socially monogamous (Schuster and Schuster 1985), a mating system often associated with even or female biased dispersal sex-ratios (Greenwood 1980, Greenwood and Harvey 1982). Indeed, both sexes have been observed while engaged in territorial defense, although *O. disjunctus* males have a greater repertoire of aggressive acoustic signals (Schuster 1983). The finding that displacement rates were similar for males and females indicates that males and females have similar dispersal ability in addition to similar dispersal rates.

**Conclusion**

Although simplistic models are often adequate when describing animal movement (Kareiva and Shigesada 1983, Bergman et al. 2000), accurate prediction of *O. disjunctus* dispersal will require the inclusion of temperature- and habitat-specific movement, edge behavior, and temporal autocorrelation in movement behavior. The complexity of the relationship between habitat and *O. disjunctus* movement behavior was indicated by the unexpected finding that movements were faster and more linear in suitable habitat. My results also support the growing body of literature (e.g., Ranius and Hedin 2001, Starzomski and
Bondrup-Nielsen 2002, Jonsell et al. 2003) that demonstrates the importance of landscape structure on movement.

Normally the slow motility in open fields, reluctance to leave forested habitat, and limited flight activity observed for *O. disjunctus* would lead to concern about population persistence in the face of recent intensive habitat fragmentation. The interesting paradox for *O. disjunctus*, however, is that the species is both common and abundant, in spite of these challenges. For example, *O. disjunctus* was found in each of 24 forest patches surveyed in the Mississippi river alluvial floodplain of Louisiana – an area distinctive in Louisiana for its particularly high forest fragmentation due to agriculture (H.B.J., unpublished data). Two non-mutually exclusive hypotheses might explain this pattern. First, *O. disjunctus* population numbers may be particularly large and stable, allowing for persistence in small, isolated patches. This is supported by the species’ relatively long life span, overlapping generations, and occupancy of coarse woody debris during all life stages (a habitat that is relatively impervious to environmental fluctuations in temperature and moisture). The population stability hypothesis would also be suggested if future studies demonstrate little to no time lag in the response of demographic rates to population density, if population numbers are stable over time, or if occupancy rate among coarse woody debris is high. Furthermore, I would expect saproxylic insects with shorter life spans, higher population turnover, and less fidelity to coarse woody debris during all life stages to be more vulnerable to population fluctuations. Second, *O. disjunctus* may engage in enough inter-forest dispersal to maintain stable, high-occupancy metapopulations. This would be supported if long distance dispersal or interpatch movement is inferred in a population genetic analysis. Given the clear limitations of *O. disjunctus* terrestrial movements, I predict that rare flight is the likely mechanism for this hypothesized dispersal.
A better understanding of *O. disjunctus* success could yield insights into the relative importance of within-forest processes (i.e., local population dynamics and among-log dispersal) versus among-forest processes (e.g., among-forest dispersal) when predicting saproxylic insect persistence. Demographic and dispersal characteristics, therefore, represent important gaps in the study of saproxylic insect conservation.
Chapter 3: Determining the Scale of Ecological Processes Affecting Incidence: From Logs to Landscapes

INTRODUCTION

Species incidence is influenced by environmental conditions (Hutchinson 1957), dispersal behavior (Brown and Kodric-Brown 1977, Pulliam 1988, Hanski 1994), and intra- and inter-specific interactions (Hardin 1960, Connell 1961, Fretwell 1972). Determining which factors are most important to incidence is made difficult by the fact that the multiple processes affecting incidence operate at different spatial and temporal scales. For example, Pinto and MacDougall (2010) showed that despite strong deterministic responses of violets to environmental quality during controlled experiments, dispersal limitation prevented strong matching between incidence and optimal environmental conditions at coarse scales (100-200 m) and low environmental predictability prevented habitat matching at fine-scales (<30 m). Studies that combine multi-scale observations of incidence with experimental work are rare, but are key to understanding the relative importance of factors influencing incidence across scales.

Recognition of scale-dependence in species distribution has led ecologists to study three complementary patterns of incidence across scale: 1) the scale of response to landscape context, 2) hierarchical levels of response to environmental predictors, and 3) scales of aggregation. The study of the scale of response focuses on determining the proper scale of measurement for an environmental feature surrounding a focal patch (usually habitat abundance) as it relates to incidence or abundance (Holland et al. 2005, Gibb et al. 2008). For example, using strength of correlation between beetle abundance and forest cover measured at multiple spatial extents at 16 independent sites as the criterion, Holland et al. (2004) found that the scale of response varied by beetle species from 20 to 2000 m. Researchers studying hierarchical levels of response
investigate the relative importance of environmental features measured at nested hierarchical organizational levels (e.g., local and regional) when predicting incidence or abundance (Cushman and McGarigal 2004). This approach has the advantage of incorporating multiple environmental features and scales simultaneously, allowing for explicit consideration of their relative importance. Instead of measuring the same feature at different spatial extents, features are organized by biologically relevant hierarchical levels (e.g., level 1 = tree characteristics, level 2 = forest characteristics). Note the use of “level” to refer to a categorical tier in a hierarchical system and “scale” to refer to a continuous gradient across spatial extents (sensu Cushman and McGarigal 2004). Cushman and McGarigal (2004), for example, showed that although at the home range level environmental features were strongly correlated with changes in bird community composition when measured in isolation, they provided little additional information when combined with much more important features measured at finer (50 m plot) and coarser (hydrological sub-basin) levels. Another source of information in hierarchical studies is the variation left unexplained by environmental features. Individuals often display a spatially aggregated distribution within each hierarchical level (= intra-class correlation), even after the association between environmental variables and incidence has been taken into account. Aggregation in incidence indicates the existence of an unmeasured process such as an unaccounted for environmental variable, dispersal limitation, or conspecific interactions, and therefore can direct researchers to the scale(s) at which mechanisms underlying incidence should be investigated.

In this study, I used all three complementary approaches to describe the scale-dependence in incidence of a saproxylic (= decayed-wood dependent) beetle, *Odontotaenius disjunctus* Illiger (Coleoptera: Passalidae). I conducted a survey of *O. disjunctus* incidence across a broad range of
spatial scales (log-sections to 3600 ha landscapes). I used this multi-scale analysis of incidence to inform the development of scale-appropriate habitat selection experiments to determine the relative importance of mechanisms underlying incidence.

*O. disjunctus* is a cursorial (walking) beetle that moves slowly (average of 36 cm min\(^{-1}\)) and avoids crossing forest boundaries (Jackson et al. 2009). I expected that incidence might be most sensitive to environmental features at fine-scales (within and among logs) within its response range (the distance at which an animal responds to environmental features), but that incidence would be patchy at large scales in association with dispersal limitation. I tested these hypotheses by relating *O. disjunctus* incidence to environmental features at four hierarchical levels (log-sections < logs < 10 m radius subplots < 0.66 ha plots) in 22 replicate landscapes in the Mississippi river valley of southern Louisiana, USA.

Because my hierarchical analyses suggested the importance of environmental variables at fine-scales when predicting incidence, I followed up my regional survey with a locally intensive survey at a single organizational level (logs). I conducted an analysis of the spatial autocorrelation among occupied logs, a measure that can indicate the spatial scale of the dispersal neighborhood. Finally, I conducted a series of experiments designed to investigate mechanisms influencing *O. disjunctus* incidence at the scales shown to be most important in my survey.

**MATERIALS AND METHODS**

**Study System**

Saproxylic beetles represent ~25% of forest beetle diversity and include a high number of red-listed species (Grove 2002 and references therein, Jonsson et al. 2006). More than 50% of bottomland hardwood forest present in the 1930s in the Mississippi river valley is gone (Rudis
and Birdsey 1986, McWilliams and Rosson 1990), most of it converted to agricultural land (MacDonald et al. 1979). Furthermore, the hydrology of the area has been aggressively altered by over 5900 km of levees built to control the Mississippi River and its tributaries (IFMRC 1994). The hydrological disruption and large variation in forest cover make this region an ideal site to investigate the influence of regional level processes on patterns of incidence.

Studies of saproxylic beetle distribution at more than one organizational level (Rukke and Midtgaard 1998, Ranius 2002, Teichert and Bondrup-Nielsen 2005, Gibb et al. 2006, Buse et al. 2007, Ulyshen and Hanula 2009) or multiple spatial extents (Økland et al. 1996, Schiegg 2000, Gibb et al. 2006) indicate the importance of log size, posture (snag or downed), decay state, and insolation for species composition at the scale of logs, and the benefits of increased volume of wood and greater forest size at landscape scales to species diversity. In this study, I expand on these studies by: 1) explicitly considering the relative importance of these features; and 2) considering four hierarchical levels of organization (instead of the usual two – logs and among logs). Furthermore, I explicitly measure the dispersal ability and intraspecific interactions that might explain mechanisms underlying incidence.

*O. disjunctus* is a large beetle (~32 mm) whose range covers eastern North America from Florida to southern Ontario and Kansas to the east coast (Schuster 1978). Although excellent descriptions of *O. disjunctus* natural history and social behavior exist (Pearse et al. 1936, Gray 1946, Schuster 1975a, Schuster 1983, Schuster and Schuster 1985, King and Fashing 2007, Wicknick and Miskelly 2009), patterns of *O. disjunctus* incidence have not been previously well-described, nor have those of any of the 700-1000 species in the family Passalidae (but see Galindo-Cardona et al. 2007). Socially monogamous *O. disjunctus* pairs create extensive galleries in wood in which they care for their offspring into adulthood (Schuster and Schuster
1985), a process that takes about three months during the summer (in North Carolina, Gray 1946). During this time they are seldom found outside of logs (Jackson et al. 2009), and presumably leave the log later only to find a new breeding territory. The process of mate and habitat location is not well-understood, but some evidence suggests that one beetle, either male or female, initiates a gallery and is joined by a mate within a few days (Schuster 1975a). Extremely rare flight has been documented (Hunter and Jump 1964, MacGown and MacGown 1996), but the vast majority of movements are cursorial (Jackson et al. 2009). Movement is especially slow in non-forest habitat which is generally avoided (beetles exhibit a strong reflection response to forest boundaries, Jackson et al. 2009). Lifespan of *O. disjunctus* is unknown, but is probably between 2 and 5 years (Gray 1946, Schuster and Schuster 1997), which encompasses 2-5 breeding seasons.

**Study Design**

**Multi-Scale Regional Survey**

I assessed *O. disjunctus* incidence in 22 forested plots in the Mississippi river valley in March – May 2006 (Figure 3.1a, see Appendix 1 for site information). Plot locations were selected to maximize variation in surrounding forest cover. In order to ensure independence in landscape level measurements, the minimum distance among sites was 20 km (lack of spatial autocorrelation among plots was confirmed using a variogram in residual analysis). This area is classified as oak-gum-cypress forest by the USDA Forest Service (Smith et al. 2004). Dominant trees in this region include *Nyssa sp.* (tupelo), *Liquidambar styraciflua* (sweetgum), *Quercus sp.* (oak), and *Taxodium sp.* (cypress).
Figure 3.1 a) Location of 22 plots (dark grey squares) in the Mississippi river alluvial floodplain (medium grey shading) in Louisiana. Parish lines are displayed in light grey. b) Arrangement of four 10-m radius subplots within which all logs were surveyed for *O. disjunctus*. Dotted lines indicate distances between plot centers.

Sampling was conducted at four hierarchical organizational levels (plot > subplot > log > log-section; Figure 3.1b). Thirty-six meters separated subplot centers in an arrangement similar to the one used by the USDA Forest Service for their Forest Inventory and Analysis (Burkman 2005, Figure 3.1b). Only logs that were suitably large (diameter ≥ 5 cm; length ≥ 1 m), decayed (decay class > 1), and hardwood (e.g., not cypress) were inspected for beetles. These restrictions were based on published (Gray 1946) and personal observations (H.B.J.) on the limits to *O. disjunctus* habitat use. I sampled up to three equal-surface area (31.4 dm$^2$) sections per log (small end, middle, large end). I controlled for surface area rather than volume because *O. disjunctus* tends to create galleries in the outermost layers of wood where decay is more advanced, and extends galleries along the length of the log rather than toward the center (H.B.J, personal observation). My selection of 31.4 dm$^2$ as the smallest sampling unit is based on preliminary sampling of logs which suggested that a log with the approximate dimensions of 10 cm diameter X 1 m length was the smallest inhabited by *O. disjunctus* (H.B.J. unpublished data). I used a
hatchet to sample each section for two minutes, and considered *O. disjunctus* present if individuals or fresh galleries were found.

I measured environmental variables that I expected to influence *O. disjunctus* incidence. At the log-section level, I recorded the presence of large wood-boring insects likely to compete with *O. disjunctus* for space. I recorded the presence of ants (in the genus *Camponotus*, *Crematogaster*, *Lasius*, *Myrmecina*, *Pheidole*, *Solenopsis*, or *Temnothorax*), termites (*Reticulitermes* sp.), and/or other large wood-boring beetles (usually Cerambycidae and Buprestidae larvae). Decay stage was classified according to five classes used by the USDA Forest Inventory and Analysis (Woodall and Williams 2005), where decay class 1 logs are sound and recently fallen and decay class 5 logs have well-decayed sapwood and heartwood and little structural integrity. In addition, the absence of heartwood due to heart rot was recorded (Woodall and Williams 2005). The diameter of each section of log was measured to the nearest cm. For each log I recorded the number of 31.4 dm$^2$ sections in the log and the position of the log (downed or standing). *O. disjunctus* is found in most if not all hardwood species in the southeastern U.S. (Gray 1946). Because of the difficulty in identifying the tree species of moderately to well-decayed logs (most logs), I omitted tree species from my analysis. At the subplot scale, the percent cover provided by the canopy was estimated from the center of each subplot based on visual inspection. Basal area (m$^2$/ha) of hardwoods was estimated in each subplot using angle count sampling (a count of trees surrounding a fixed point which are larger than an object held at arms length from the eye, Bitterlich 1948, Bay 1960) with basal area factor of 10. At the plot level, amount of wood in decay class 2 or greater was summed across subplots and was measured in units of 31.4 dm$^2$ sections per sampling area. The volume of wood within subplots was strongly correlated with log size at the log level and was therefore not considered.
As an indicator of flooding susceptibility, the presence of levee protection was gathered from flood gage data (http://waterdata.usgs.gov) and personal interviews with each landowner and/or manager. Regular flooding occurs at three of the sampled sites: Cat Island, the southern plot in the Sherburne Wildlife Management Area, and at Grand Cote National Wildlife Refuge.

Table 3.1 Parameters measured in the multi-scale regional survey of *O. disjunctus* occupancy. Continuous and categorical data are summarized by plot (e.g., mean proportion of log sections in a category per plot).

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Abb.</th>
<th>Mean</th>
<th>SD</th>
<th>Min</th>
<th>Max</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Log Section (31.42 dm² surface area each, n = 1161)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>O. disjunctus</em> present</td>
<td>occ</td>
<td>0.19</td>
<td>0.14</td>
<td>0.00</td>
<td>0.46</td>
</tr>
<tr>
<td>termites present</td>
<td>trm</td>
<td>0.18</td>
<td>0.10</td>
<td>0.03</td>
<td>0.38</td>
</tr>
<tr>
<td>ants present</td>
<td>ant</td>
<td>0.47</td>
<td>0.13</td>
<td>0.23</td>
<td>0.71</td>
</tr>
<tr>
<td>other wood boring beetles present</td>
<td>btl</td>
<td>0.19</td>
<td>0.12</td>
<td>0.00</td>
<td>0.47</td>
</tr>
<tr>
<td>decay class</td>
<td>dec</td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>2</td>
<td></td>
<td>0.28</td>
<td>0.10</td>
<td>0.08</td>
<td>0.54</td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>0.43</td>
<td>0.10</td>
<td>0.31</td>
<td>0.64</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td>0.26</td>
<td>0.10</td>
<td>0.09</td>
<td>0.42</td>
</tr>
<tr>
<td>5</td>
<td></td>
<td>0.03</td>
<td>0.05</td>
<td>0.00</td>
<td>0.19</td>
</tr>
<tr>
<td>hollow due to heart rot</td>
<td>hol</td>
<td>0.11</td>
<td>0.08</td>
<td>0.04</td>
<td>0.37</td>
</tr>
<tr>
<td>log diameter (cm)</td>
<td>wid</td>
<td>17.13</td>
<td>2.38</td>
<td>12.63</td>
<td>22.70</td>
</tr>
<tr>
<td>b) Log (lengths vary, n = 629)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>number of 0.314 m² sections per log</td>
<td>sz</td>
<td>7.31</td>
<td>2.02</td>
<td>4.24</td>
<td>10.75</td>
</tr>
<tr>
<td>position (0 = downed, 1 = standing)</td>
<td>sng</td>
<td>0.07</td>
<td>0.06</td>
<td>0.00</td>
<td>0.21</td>
</tr>
<tr>
<td>c) Subplot (10 m radius each, n = 88)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
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<tr>
<td>canopy closure (proportion)</td>
<td>can</td>
<td>0.72</td>
<td>0.10</td>
<td>0.52</td>
<td>0.90</td>
</tr>
<tr>
<td>basal area of hardwood trees (m²/ha)</td>
<td>G</td>
<td>84.5</td>
<td>12.08</td>
<td>60.68</td>
<td>105.80</td>
</tr>
<tr>
<td>d) Plot (4 subplots each, n = 22)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>levee protected</td>
<td>lev</td>
<td>0.86</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>proportion of surrounding 225 ha forested</td>
<td>for</td>
<td>0.65</td>
<td>0.25</td>
<td>0.18</td>
<td>0.96</td>
</tr>
<tr>
<td>fragmentation of forest cover in 225 ha forest</td>
<td>frg</td>
<td>0.27</td>
<td>0.15</td>
<td>0.02</td>
<td>0.65</td>
</tr>
</tbody>
</table>

For each plot, I also quantified the amount of suitable forest habitat surrounding the plot.

Land use data were downloaded from the United States Geological Survey online database (sabdata.cr.usgs.gov, USGS 1998). With 30 by 30 meter grid cells, these data categorized land use into 23 categories which I simplified into two: forested or non-forested. Most of the non-forested areas in this region were either water or agriculture. Jackson et al. (2009) demonstrated
that beetles are unlikely to disperse through open habitats and thus the amount of non-forested habitat is likely to restrict movement and reduce incidence. I considered land use patterns of four increasingly larger square regions around each plot (52 ha, 225 ha, 900 ha, 3600 ha, square plots instead of circles were used for ease of calculation in ArcGIS). The land use information for each region around each plot was converted into grid format in ArcGIS 9.3. Proportion forested (“PLAND” in Fragstats) and fragmentation (the inverse of “CLUMPY” in Fragstats) was measured using Fragstats 3.3 (McGarigal et al. 2002). The configuration of forested habitat within each square region was calculated. Predictor variables are summarized in Table 3.1.

**Intensive Within-Forest Census**

In April and early May of 2005, an intensive within-forest census was conducted which more thoroughly described the relationship between *O. disjunctus* incidence and two spatial factors: the spatial distribution of logs and conspecifics. All suitable (diameter >= 5 cm; length >= 1 m, decay class > 1, hardwood) logs (n = 666) within a 250 X 250 m plot (6.25 ha) of mixed hardwood forest were inspected for the presence of *O. disjunctus*. The plot was located at Port Hudson State Historic Site (661869 easting, 3396466 northing, Zone 15, WGS84) approximately 30 km northwest of Baton Rouge, Louisiana. Port Hudson is a 244 ha secondary mesic forest located on loess slopes just east of the Mississippi River. Length, small and large end diameter, decay class, orientation (cardinal direction from large to small end) and position (snag or downed) of each suitable hardwood log was recorded, and its location was measured using a TRIMBLE GeoXT GPS outfitted with an external antenna (positional accuracy of < 0.5 m). *O. disjunctus* was considered present if: a) fresh “sawdust” distinctive of *O. disjunctus* was found under the log (distinguished from ant-made sawdust by its coarser grain); or b) hatchet-aided investigation revealed fresh *O. disjunctus* galleries and/or the beetle itself.
**Response-Range Experiment**

In March 2008, I evaluated the response range (the distance at which an animal responds to an environmental feature, Fletcher and Sieving 2010) of *O. disjunctus* by placing beetles 1-3 m from a log and evaluating whether movement toward the log was greater than expected by chance. Three logs were used in my trials, each from the same tree (red oak) and of similar decay (early decay class 3). None of the logs had been occupied previously and each was approximately 40 cm long and 20 cm in diameter. The logs were placed in a clearing within a forest at Burden Research Plantation (681667 easting, 3365955 northing, Zone 15, WGS84), each at least 10 m from any other log or tree. Each beetle (*n*=14) was tested twice, once at one meter and once at three meters from the log. Beetles were randomly assigned to a different log for each distance. To prevent agitation dispersal (rapid movement in response to handling, Turchin 1998), I set each container on its side and allowed the beetle to exit the container on its own. The container was set on the ground in a position neutral with respect to the log. The beetle was observed until it moved one meter from its release point at which time its move was scored as either toward or not toward the log. To be considered a move toward the log, the end location of the beetle had to be within the angle subtended by the patch (the smaller angle subtended by a log 3 m distant was accounted for statistically; see “Statistical Methods”; Haddad and Baum 1999).

**Habitat Selection and Movement Experiment**

I tested the hypotheses that a) conspecifics and/or b) large log size increased the probability of immigration, decreased the probability of emigration, and resulted in higher overall abundance of beetles in a log one week after release into logs. Beetles were released at different abundances (0, 1, 2, ≥ 3 beetles) within small (range = 7-11 cm, ~11.3 dm² surface
area) and large (range = 16-28 cm, ~27.7 dm$^3$ surface area) logs. The smallest logs were selected to have less surface area than any log occupied in my surveys (smallest occupied log = 26.0 dm$^2$) in order to test whether a) beetle absence in small logs was due to choice (as opposed to low reproductive success) and b) if small logs were less preferred, could attraction to conspecifics override aversion to small log size (Stamps 1988). Two red oaks (Quercus sp.), which had experienced 3 years of decay and were in decay class 3, were cut into 40 cm long logs. In order to allow beetle galleries to be inspected without further damaging the log or harming the inhabitants, I followed a procedure modified from Hernandez-Martinez and Castillo (2003). Here, each log was sliced longitudinally into 3 cm thick slices and the slices were held together with rubber tubing to form a complete log. Experimental logs were placed in two 36 X 36 m grids, one in Louisiana State University’s Burden Research Plantation (hereafter Burden) and the other in Louisiana State University’s Central Research Station (hereafter CRS). Logs were spaced 6 m apart, a distance selected to minimize detection of nearby logs (see Results for response range experiment). All naturally occurring woody debris with diameter greater than 5 cm was removed from the plots.

Prior to conducting the experiment, the thoraces of all beetles were marked using an insect pin such that they could be individually identified (Gray 1946). All experimental beetles were collected from the surrounding forest and randomly assigned to a log. Zero beetles ($n = 32$ small logs, 19 large logs), a single beetle ($n = 20$ small logs, 35 large logs), two beetles of opposite sex ($n = 13$ small logs, 6 large logs), or more than two beetles ($n = 6$ small logs, 12 large logs) were added to each log. These logs were generated from a separate study (H.B.J., unpublished data) that had unequal sample sizes. Each log was taken apart one week after the log was removed from its bin and the identity and location of beetles were recorded. Therefore,
my data were limited to two points in time, and I had no information concerning the order in
which beetles emigrated from or immigrated into logs during the intervening week. The distance
each recaptured beetle travelled from its release location was used to quantify a redistribution
kernel for *O. disjunctus*. The same experiment was performed twice (with different beetles each
time) on all logs, once in May of 2008 and again in June of 2008.

**Performance Experiment**

An experiment testing the effects of conspecific density and log diameter on finite
population growth rate ($N_{Nov, N_{June}^{-1}}$) was performed at Ben Hur between June and November
2008 (long enough for one complete breeding season). I measured finite population growth rate
(the number of adults in November included adult offspring of those released in June), in
addition to component demographic variables fecundity, juvenile survival, and adult survival. I
focus on finite population growth rate here, but detail fecundity, juvenile survival, and adult
survival in Appendix 2. The logs were the same ones used in the selection experiment: small
diameter (range = 7-11 cm, ~11.3 dm$^3$ surface area) and large diameter (range = 16-28 cm,
~27.65 dm$^3$ surface area). Beetles collected from the surrounding forest were randomly assigned
to logs at abundances of one ($n = 12$, 6 small logs and 6 large logs), two ($n = 12$, 6 small logs and
6 large logs), or three male/female couples ($n = 6$, large logs only). I placed the logs in 38 L
plastic bins (50 length by 12 width x 33 height cm) with a 2 cm thick layer of newspaper lining
the bottom to retain moisture. Bins had 7 cm diameter holes in the top covered with screen to
allow ventilation and small drainage holes drilled in the bottom, but were otherwise sealed to
prevent emigration or immigration. I placed beetles in the logs on June 20, 2008. Bins were left
undisturbed except for two censuses, one at 80 days, and the other at 157 days after the
experiment began. The first census was timed to be able to count juveniles and the timing of the
second census allowed offspring sufficient time to mature to adulthood (Gray 1946). Two bins were damaged during Hurricane Gustav (September 1, 2008) and were not included in the analyses described below.

**Statistical Methods**

**Multi-Scale Regional Survey**

Multi-level analysis included the following steps: 1) single-level analysis at the plot scale to determine the scale of response of incidence to forest cover, 2) single-level analyses at each of four hierarchical levels to determine the most important predictors to be used in multi-level analyses, 3) model selection comparing many multi-level regression models, 4) model-averaging of raw coefficients among the best set of models, 5) comparison of relative importance of environmental predictors using hierarchical variance partitioning, 6) comparison of relative importance of environmental predictors using scaled regression coefficients, 7) evaluation of variance components to determine autocorrelation (after environmental predictors had been factored out) at each level. I expected to find a large importance of forest cover at the plot level and large autocorrelation at scales where dispersal is limiting (subplot and plot).

I evaluated the scale of response of incidence to forest cover using an optimization method similar to that described by Holland et al. (2004). Four logistic regression models relating forest cover to the logit-transformed proportion of *O. disjunctus* occurrence among sections in a plot were created - one for each spatial extent (51.84 ha, 225 ha, 900 ha, or 3600 ha). Proportion forested required a logit-transformation to achieve normality. Whereas Holland et al. (2004) suggested measuring only the bivariate relationship between habitat cover and population incidence for their optimization routine, I also included the presence of levees and a fragmentation index (rank transformed to achieve normally distributed residuals) in my model.
An interaction between fragmentation and forest cover was included because of the hypothesis that fragmentation will be more important to population persistence (and presumably incidence as well) when habitat cover is low (Fahrig 1998). The scale with the best model fit was selected based on the lowest Akaike information criterion values adjusted for small sample size (AICc) (Sugiura 1978, Hurvich and Tsai 1989). The analysis was performed in R (R Development Core Team 2010).

As recommended by Cushman and McGarigal (2002, 2004), I reduced the number of predictors before conducting the hierarchical analysis by creating single-level logistic regression models at each sampling level (section, log, subplot, and plot). I selected the best predictors based on the models with the lowest AICc value. At the section level, the response variable was a binary value indicating whether the section was occupied by at least one passalid beetle. At each of the other three levels the response was the logit-transformed proportion of sections occupied at that level (mean number of sections = 1.9 per log, 13.2 per subplot, 51.6 per plot). Models with all possible combinations of predictor variables (see Table 3.1) at each scale were compared (64 section level models, 4 log level models, 4 subplot level models, and 10 plot level models). Bole diameter and number of sections per log required a ln-transformation.

Once uninformative predictors had been removed, I combined the best predictors from the single-level analyses into one multi-scale logistic regression mixed effects analysis. This analysis included plot, subplot, and log as nested, random effects (plot > subplot > log), thereby taking autocorrelation within these spatial scales into account (lme4 package in R, Bates et al. 2008). I used the Laplacian approximation to estimate the marginal distribution of the response (incidence), an estimate that yields an approximate maximum likelihood score (Vonesh 1996) and does not produce the biased estimates sometimes observed with the penalized-quasi
likelihood method (Li et al. 2008). I considered all combinations of predictors from the single level analyses, which had a summed Akaike weight ($\sum w_i$, interpreted as the probability that a predictor is in the true model, Burnham and Anderson 2004) of 0.5 or greater (9 predictors, 512 models total). Canopy cover was strongly collinear with all three variables measured at the plot level (see correlation matrix in Appendix 3). To reduce collinearity and to evaluate the importance of canopy cover after plot level variables were factored out, I used the residuals of the regression of canopy cover on plot level variables as a predictors in the multi-level analysis. Pearson’s correlation statistics among other independent variables used in the multi-level analysis did not exceed an absolute value of $r = 0.14$.

During the model selection process, models with AIC$_c$ scores similar to the best model ($\Delta$AIC$_c < 2$) were considered informative (Burnham and Anderson 2004). To incorporate the information contained in multiple models, all models with $\Delta$AIC$_c < 2$ were averaged together following the methods of Burnham and Anderson (2004). The averaged estimates for means and standard errors were weighted averages based on the Akaike weights of each model. Akaike weights ($w_i$) can be interpreted as the probability that a model is the “true” model. Model averaging often results in greater predictive accuracy (Madigan and Raftery 1994) and represents a powerful solution to model uncertainty, a challenge which is considered relevant for models of species distribution (Elith and Leathwick 2009).

I next tested the hypothesis that the relationship between incidence and environmental variables was strongest at fine-scales within its response range. Specifically, I predicted that environmental variables measured at the log-section and log levels would explain a greater proportion of variance in incidence than variables measured at subplot and plot levels and would have a stronger relationship with incidence as measured by regression coefficients. The relative
variation explained independently by each predictor variable included in the full multi-scale model was assessed using the algorithm outlined by Chevan and Sutherland (1991) (hier.part package in R, Walsh and MacNally 2008). Basically, this algorithm averages the change in $R^2$ when the variable in question is dropped from all nested models of the full model. I used Nagelkerke’s pseudo-$R^2$ ($R^2_N$, Nagelkerke 1991) as an estimate of goodness of fit that is appropriate for general linear models. Nagelkerke’s pseudo-$R^2$ was calculated for models incorporating every combination of fixed variables nested within the best model (512 models) – all three random effects were included in all of these models. Although $R^2_N$ cannot be interpreted as an absolute measure of explained variance (Long 1997), it can be used as an estimate of the improvement in the model relative to the null model. I calculated two $R^2_N$ values for the best model(s): one compared with the random effects only model (referred to as the conditional $R^2_N$ value, Vonesh and Chinchilli 1997) and the other compared with the intercept only model (e.g., marginal $R^2_N$ value). These values tended to be similar, and I report only the latter because it may provide a better estimate of the significance of fixed effects (Orelien and Edwards 2008).

Comparison of relative importance using effect size was made difficult by three characteristics of my data: 1) continuous predictors were measured on different scales, 2) many predictors were binary, and 3) all three continuous predictors were transformed. To address these problems I standardized each input variable by subtracting the mean and dividing by the standard deviation before analysis. The resulting standardized coefficient is interpreted as the change in incidence associated with a one standard deviation change in a given independent variable (Menard 2004).

Finally, I identified the hierarchical level at which the greatest aggregation in incidence occurred (i.e., highest intra-class correlation), even after underlying environmental filters were
taken into account. The level at which this underlying patchiness in incidence occurred was the key piece of information I used to determine the scale of my subsequent experiments investigating potential causes for aggregation. I expected to find large unexplained aggregation in incidence at the plot and subplot levels because I expected dispersal limitation to create a patchy distribution at those scales. The random effects estimates provided by my hierarchical model were the starting point for this analysis. Confidence intervals for random effects were estimated using 1000 posterior simulations ("arm" package, Gelman and Hill 2006). The random effect sizes indicate the extent to which variation in incidence varied among units within a hierarchical level (among plots, among subplots, among logs). The greater the random effects estimate, the greater the correlation in incidence at that level. A limitation of mixed-effects logistic regression is that the random effect sizes cannot be directly compared with the residual error, because the random effect sizes are constant, but the residual error in logistic regression varies nonlinearly with the predicted values, P, according to the equation P(1-P). In order to compare the random variation at each level (correlation within plots, subplots, or logs) to the residual variation (independent variation among sections), I used a simulation procedure developed by Goldstein (2002) and Li et al. (2008). Briefly, I used my model averaged estimates of fixed effects and the variation associated with each random effect to simulate expected incidence of sections (P*) and the associated residual variation (= P*(1-P*)). This simulation allowed a direct comparison of the within and among-group variation for a range of predicted values. I simulated observed incidence probabilities using 50 replicates at each spatial scale (total replicates = 125,000) for each of 101 predicted incidence probabilities between 0 and 1. The random (among plots, subplots, logs) and the residual variation (among sections) were then on the same scale and could be compared directly.
Intensive Local Census

The spatial arrangements of logs and occupied logs were described using Ripley’s L-function, an estimate of how the intensity of a point process differs from a random Poisson process (Kaluzny et al. 1989). The significance of the difference from a random process was estimated over distances between 0 and 100 meters using Monte Carlo simulations with 1000 replicates (package "spatial", Venables and Ripley 2002).

I tested the hypotheses that spatial scale of response of *O. disjunctus* incidence to proximity of 1) other logs occupied by conspecifics and 2) other logs in general is small (m) using autologistic regression. “Autologistic” or “autocovariate” models (Augustin et al. 1996, Dormann et al. 2007) use a covariate that is very similar to the isolation index developed by Hanski (1994) (See Appendix 4). The autocovariate function is a distance-weighted average of the number of occupied (hypothesis 1: conspecific proximity) or total (hypothesis 2: log proximity) logs surrounding a focal log. It requires an estimate of the dispersal neighborhood, or the distance from which the factor of interest (number of occupied logs or total number of logs) might have an effect. I used an optimization routine recommended by van Teeffelen and Ovaskainen (2007) to find the best parameterization for the two autocovariate functions. I tested a broad range of dispersal neighborhood estimates for their ability to improve the fit of a logistic model predicting *O. disjunctus* incidence. All models included predictor variables log size (ln-transformed number of 31.42 dm² sections in a log), decay class, log position (downed or standing), the slope of terrain, and the x,y coordinates of each log. Instead of modeling decay class as a categorical variable (as in the regional survey), I modeled decay class as a continuous variable to reflect the multiple stages of decay represented by different sections of a single log. I included the quadratic term for decay class to take into account the expected non-linear
relationship between decay and incidence (Gray 1946). The model with the best dispersal
neighborhood estimate was selected based on its AICc value (see Appendix 4 for details). This
optimization was performed separately for the conspecific proximity autocovariate and the log
proximity autocovariate.

Once the best parameterizations for both autocovariates were selected, I tested the
hypothesis that *O. disjunctus* incidence is more closely associated with the distribution of
conspecifics than with the distribution of logs. The full model included both autocovariates and
all of the predictors described above. All combinations of predictors were tested (512 models)
and the estimates from the best set of models were averaged as described previously.

**Response Range Experiment**

I tested the hypothesis that the response range of *O. disjunctus* is less than 3 meters but
greater than 1 meter. Exact binomial tests were used to determine whether movement toward a
log was more frequent than by chance given the horizon occupied by the log. A log one or three
meters away constituted 8.3% or 4.4% of a beetle’s horizon, respectively. I used a paired t-test to
test the hypothesis that directed movement toward a log was more frequent at one meter than at
three meters.

**Habitat Selection and Movement Experiment**

I tested the effect of log size and the original number of beetles in the log on three
outcomes related to habitat selection: 1) the proportion of original beetles that emigrated; 2) the
probability of immigration of one or more beetles from another log; and 3) the final number of
adults in the log one week after release. To evaluate the emigration and immigration I used
logistic regression and the final number of beetles was predicted by Poisson regression. Log size
(small or large), original number of beetles (0, 1, 2, ≥ 3) and their interaction were predictors.
Only logs which were originally occupied were used to predict probability of emigration (n = 92). The immigration test included all logs (n = 143) and the analysis of the final number of beetles included only those logs with one or more beetle at the end (n = 54). No variation between sites (Ben Hur and Burden) or months (May and June) were detected and these data were pooled.

I developed a redistribution kernel for the 60 (out of 210) beetles that were recaptured during this experiment. I divided the observed dispersal distances into six 5-m wide distance classes from 0 m to 30 m. The number of beetles in each distance class was weighted by the number of experimental logs available to each beetle in that distance class according to the equation

\[ N_d = \sum_{i=1}^{n_d} \frac{1}{CWD_{id}} \]  

where \( N_d \) = the adjusted number of beetles per distance class \( d \), \( n_d \) = the actual number of beetles per distance class \( d \), \( CWD_{id} \) is the number of logs available to each beetle at the distance class in which they were recaptured. By summing these weighted scores for each distance class I created a dispersal distribution that took the trap (log) arrangement into account. I compared the ability of two models to predict the ln-transformed weighted density of beetles at each distance class: a) an exponential distribution such that raw distance was the predictor; and b) a power distribution such that the ln-transformed distance was the predictor. Both distributions suggest “fat” tails (high numbers of long-distance dispersers) relative to a Gaussian distribution, but the tail is fatter (i.e., more long distance dispersers) in a power distribution (Turchin 1998). This shape of the redistribution kernel is important because fat-tails can have large-scale implications for the distribution of a species (Kot et al. 1996).
Performance Experiment

I tested the hypotheses that log size and conspecific density improve beetle finite growth rate. To meet the assumption of normality, finite growth rate was ln-transformed

$$\ln \left( N_{\text{Nov}}N_{\text{Sept}}^{-1} + 0.50 \right).$$

Predictor variables were log size (small or large) and number of females (categories 1, 2, 3). All combinations of variables were considered including an intercept only model (4 models).

RESULTS

Multi-Scale Regional Survey

*O. disjunctus* was common, occurring in all but one of the forest plots and occupying an average of 0.19 (95% parametric CI = 0.17-0.21) of suitable log-sections, 0.26 (0.22-0.29) of logs, 0.73 (0.62-0.81) of subplots, and 0.95 (0.75-1.00) of plots. In my test of the scale of response to forest cover, I found that forest cover was most informative (according to AICc) when measured at 225 ha ($w_i$ [Akaike weight] = 0.58; compared with three other models with

<table>
<thead>
<tr>
<th>Spatial Extent (ha)</th>
<th>for</th>
<th>frag</th>
<th>for X frag</th>
<th>lev</th>
<th>k</th>
<th>$\Delta$AIC$_c$</th>
<th>$w_i$</th>
<th>$R^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>3600.0</td>
<td>-1.38 (0.42)</td>
<td>0.15 (0.18)</td>
<td>1.58 (0.40)</td>
<td>1.36 (0.30)</td>
<td>5</td>
<td>4.88</td>
<td>0.05</td>
<td>94.0%</td>
</tr>
<tr>
<td>900.0</td>
<td>-0.84 (0.43)</td>
<td>-0.04 (0.20)</td>
<td>1.18 (0.43)</td>
<td>1.34 (0.30)</td>
<td>5</td>
<td>2.13</td>
<td>0.20</td>
<td>92.2%</td>
</tr>
<tr>
<td>225.0</td>
<td>0.14 (0.32)</td>
<td>0.10 (0.22)</td>
<td>0.54 (0.34)</td>
<td>1.40 (0.30)</td>
<td>5</td>
<td>0.00</td>
<td>0.58</td>
<td>94.8%</td>
</tr>
<tr>
<td>51.8</td>
<td>0.24 (0.17)</td>
<td>1.51 (0.30)</td>
<td>2.41</td>
<td>0.17</td>
<td>87.9%</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The best model is in bold. $\hat{z}$=standardized regression coefficient (SE), k=number of parameters, $\Delta$AIC$_c$=change in Akaike information criterion adjusted for small sample sizes, $w_i$=Akaike weight indicating probability that a model is the “true” one, $R^2_n$=Nagelkerke pseudo-$R^2$. Forest cover (for) is logit-transformed and the fragmentation index (frag) is rank-transformed. Levees (lev) are present or absent.
Table 3.3 Test of the relative importance of environmental variables measured at multiple organizational levels when predicting the incidence of *O. disjunctus* in log sections (nplot = 22, nsubplot = 88, nlog = 629, nsections = 1161).

a) Model-averaged fixed effect estimates

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\bar{x}$ (SE)</th>
<th>$\hat{z}$</th>
<th>$\sum w_i$</th>
<th>$iR^2_n$</th>
<th>$jR^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta_0$</td>
<td>-7.11 (0.81)</td>
<td></td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_{dec}$</td>
<td>3</td>
<td>2.21 (0.34)</td>
<td>1.09</td>
<td>1.00</td>
<td>9.9%</td>
</tr>
<tr>
<td>$\beta_{hol}$</td>
<td>4</td>
<td>2.51 (0.36)</td>
<td>1.10</td>
<td>1.00</td>
<td>9.9%</td>
</tr>
<tr>
<td>$\beta_{ant}$</td>
<td>5</td>
<td>1.27 (0.74)</td>
<td>0.22</td>
<td>1.00</td>
<td>9.9%</td>
</tr>
<tr>
<td>$\beta_{btl}$</td>
<td>6</td>
<td>-1.04 (0.39)</td>
<td>0.33</td>
<td>1.00</td>
<td>1.1%</td>
</tr>
<tr>
<td>$\beta_{sz}$</td>
<td>7</td>
<td>0.55 (0.10)</td>
<td>0.54</td>
<td>1.00</td>
<td>3.1%</td>
</tr>
<tr>
<td>$\beta_{can}$</td>
<td>8</td>
<td>-0.93 (0.45)</td>
<td>0.24</td>
<td>1.00</td>
<td>0.2%</td>
</tr>
<tr>
<td>$\beta_{lev}$</td>
<td>9</td>
<td>-2.87 (1.41)</td>
<td>-0.27</td>
<td>0.81</td>
<td>0.3%</td>
</tr>
<tr>
<td>$\beta_{for}$</td>
<td>10</td>
<td>2.85 (0.71)</td>
<td>1.03</td>
<td>1.00</td>
<td>1.7%</td>
</tr>
<tr>
<td>$\beta_{sz}$</td>
<td>11</td>
<td>0.33 (0.16)</td>
<td>0.42</td>
<td>1.00</td>
<td>1.2%</td>
</tr>
</tbody>
</table>

b) Random-effect estimates

<table>
<thead>
<tr>
<th>Level</th>
<th>$\sigma_R$ (95CI)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Log</td>
<td>0.73 (0.69-0.77)</td>
</tr>
<tr>
<td>Subplot</td>
<td>0.84 (0.73-0.96)</td>
</tr>
<tr>
<td>Plot</td>
<td>0.61 (0.44-0.80)</td>
</tr>
</tbody>
</table>

c) Best model set

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>$\Delta$AICc</th>
<th>$w_i$</th>
<th>$R^2_n$</th>
<th>AUC</th>
</tr>
</thead>
<tbody>
<tr>
<td>dec + ant + hol+sz + sng + can + lev + for</td>
<td>14</td>
<td>0.00</td>
<td>0.48</td>
<td>30.0%</td>
<td>0.92</td>
</tr>
<tr>
<td>dec + ant + hol+btl + sz + sng + can + lev + for</td>
<td>15</td>
<td>0.77</td>
<td>0.33</td>
<td>30.1%</td>
<td>0.92</td>
</tr>
<tr>
<td>dec + ant + hol+sz + sng + lev + for</td>
<td>13</td>
<td>1.86</td>
<td>0.19</td>
<td>29.6%</td>
<td>0.91</td>
</tr>
</tbody>
</table>

$x =$ model averaged coefficient, $\hat{z}$ = change in incidence associated with a change in one standard deviation in $x$, $\sum w_i =$ summated Akaike weight indicating probability that a predictor is in the “true” model, $iR^2_n =$ variation independently explained by a predictor, $jR^2_n =$ variation jointly explained by predictor, $\sigma_R$ median random effect and 95 percent confidence interval estimated using 1000 posterior simulations, $\Delta$AICc change in Akaike information criterion adjusted for small sample sizes, $w_i =$ Akaike weight indicating probability that a model is the “true” one, $R^2_n =$ marginal Nagelkerke pseudo-$R^2$, AUC = area under the ROC curve indicating the predictive accuracy of the model. Key to predictor abbreviations in Table 3.1. Number of log-sections per log (sz) was natural log transformed. The residuals of the regression of percent canopy cover on the presence of levees and proportion forest cover was used instead of raw canopy cover scores. Proportion of forest cover was logit-transformed.
forest measured at 52 ha, 900 ha, 3600 ha, Table 3.2). For the subsequent multi-scale analysis, I used forest cover within 225 ha as the appropriate landscape-scale parameter.

Predictors included in the final multi-scale model set with high certainty ($\sum w_i = 1$) included log-section-level variables decay class, presence of heart rot, presence of ants; log-level variables log size, log position; and plot-level variables presence of levees, and forest cover (Table 3.3). Model uncertainty surrounded the inclusion of log-section-level variable presence of other wood boring beetles ($\sum w_i = 0.33$) and subplot-level variable canopy cover ($\sum w_i = 0.81$) in the best model. The presence of termites, log diameter, and basal area of standing hardwood were eliminated from the analysis due to low information value in single-level analyses ($\sum w_i < 0.5$, Appendix 5). Fragmentation of forest cover and the interaction between fragmentation and forest cover were informative in the single-level plot analysis, but were not informative when combined with variables measured at other scales.

The best set of models provided good fit to the data (Table 3.3). Explained variance was 30.1% for the fullest of the best models and the AUC was 0.92 (indicating high predictive accuracy, Swets 1988). Two predictors, measured at the log-section and the log levels, respectively, stood out for their ability to explain passalid incidence: decay class ($iR^2_n = 9.9\%$) and log size ($iR^2_n = 3.1\%$, Table 3.3, Figure 3.2). Other predictors, among which the presence of levees (measured at the plot-level) was the most prominent ($iR^2_n = 1.7\%$), explained less than 2% of the variance each (Table 3.3). Predictors were reasonably independent of each other in their explanatory power with the exception of forest cover which had a joint explanatory power greater than its independent explanatory power ($jR^2_n = 1.9\%$, Table 3.3). All other predictors had joint explanatory power less than or equal to 0.3%.
Decay class and the presence of levees stood out for their large standardized coefficients (\( \hat{z} = 1.09, 1.10, 0.22 \) for decay classes 3, 4, and 5, respectively and \( \hat{z} = 1.03 \) for levees, Table 3.3, Figure 3.2, Figure 3.3). The relative importance of log size depends on how effect is measured: the expected change in incidence associated with one standard deviation change in log size is less than a comparable change in levees (ln-transformed log size \( \hat{z} = 0.54 \), Table 3.3). But over the full range of these predictor variables, the expected change in incidence is much greater for log size than for levees (Figure 3.3). As determined by standardized coefficients, the relative importance of other predictors was generally consistent with their explained variance (Table 3.3, Figure 3.2, Figure 3.3).
Figure 3.3 The probability that a section (0.31 m² surface area) of log located in one of 22 replicate landscapes was occupied by *O. disjunctus* was dependent on (in order of independently explained variation) a) moderate decay class, b) large log size, c) presence of a levee, d) proportion in the surrounding 225 ha that was forested, e) absence of heart rot, f) the absence of ants, g) the presence of other wood borers (mostly cerambycid beetles), h) decreased canopy cover, and i) downed position (not a snag). Values are back-transformed model-averaged estimates of least squares means and SE. Different letters indicate significant least squares differences among model-averaged means ($\alpha = 0.05$). Predictors are those deemed informative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3). In order to make graphs most representative by model selection based on AICc values (Table 3.3).
Although significant aggregation in incidence occurred at all higher levels (Table 3.3), most residuals were uncorrelated (residual variation >76% of unexplained variation, Figure 3.4). Aggregation in incidence (measured by intra-class correlation) was greatest at the subplot level (maximum = 11% of the unexplained variation, Table 3.3, Figure 3.4). Aggregation at the log and plot levels accounted for a maximum of 8% and 5% of the unexplained variation, respectively (Figure 3.4).

**Intensive Local Census**

In a 6.25 ha plot at Port Hudson, 25.4% of 666 logs were occupied. Logs were significantly clustered from all distances investigated (0 – 100 m) based on Ripley’s L-function, with no obvious peaks in autocorrelation. Spatial autocorrelation among occupied logs was greater than for logs in general, peaking at 15 meters. Decay class followed a hump-shaped
distribution with most logs in decay class 3 (46%). Only 5% of logs were standing. The median slope of the terrain was 0.13 (range: 0-2.10).

The best models relating isolation and log quality variables to incidence explained between 40.8% and 41.5% of the total variation in incidence in the Port Hudson census (Table 3.4). Incidence was most associated with the presence of occupied logs within 3.9 m (= dispersal neighborhood, Appendix 6) and with the presence of any logs within 15.5 m (Appendix 6). This

### Table 3.4 Model predicting incidence using data from a single, intensively censused 6.25 forest plot (n=666 logs).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\bar{x}$</th>
<th>$\hat{z}$</th>
<th>$\sum W_i$</th>
<th>$iR^2_n$</th>
<th>$jR^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta_0$</td>
<td>-15.24 (2.93)</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_{\ln(sz)}$</td>
<td>1.19 (0.12)</td>
<td>1.20</td>
<td>1.00</td>
<td>25.1%</td>
<td>5.5%</td>
</tr>
<tr>
<td>$\beta_{\ln(C3.9)}$</td>
<td>0.36 (0.09)</td>
<td>0.57</td>
<td>1.00</td>
<td>5.0%</td>
<td>5.0%</td>
</tr>
<tr>
<td>$\beta_{\text{dec}}$</td>
<td>7.88 (1.95)</td>
<td>0.59</td>
<td>1.00</td>
<td>4.0%</td>
<td>0.3%</td>
</tr>
<tr>
<td>$\beta_{\text{dec}^2}$</td>
<td>-1.22 (0.33)</td>
<td>-0.39</td>
<td>1.00</td>
<td>3.2%</td>
<td>0.0%</td>
</tr>
<tr>
<td>$\beta_{\ln(H15.5)}$</td>
<td>0.01 (0.03)</td>
<td>0.07</td>
<td>0.10</td>
<td>2.5%</td>
<td>4.1%</td>
</tr>
<tr>
<td>$\beta_{\text{sng}}$</td>
<td>-1.06 (0.47)</td>
<td>-0.22</td>
<td>1.00</td>
<td>0.4%</td>
<td>-0.3%</td>
</tr>
<tr>
<td>$\beta_{\text{slp}}$</td>
<td>-0.29 (0.24)</td>
<td>-0.16</td>
<td>0.46</td>
<td>0.4%</td>
<td>0.2%</td>
</tr>
<tr>
<td>$\beta_{\text{est}}$</td>
<td>0.00 (0.00)</td>
<td>-0.15</td>
<td>0.50</td>
<td>0.9%</td>
<td>0.8%</td>
</tr>
</tbody>
</table>

$\bar{x}$=model averaged coefficient, $\hat{z}$=standardized coefficient, $\sum W_i$=summed Akaike weight indicating probability that a predictor is in the “true” model, $R^2_n$=percent of $R^2_n$ independently explained by a predictor, $k$=number of parameters, $\Delta AIC_c$=change in Akaike information criterion adjusted for small sample sizes, $w_i$=Akaike weight indicating probability that a model is the “true” one, $R^2_n$=Nagelkerke pseudo-$R^2$; $sz$ = number of 27.7 dm$^2$ log-sections per log, $C_{3.9}$ = conspecific proximity with 3.9 m neighborhood size, $\text{dec}$ =mean decay of log, $H_{15.5}$ = log proximity with 15.5 m neighborhood size, $\text{sng}$ = downed (0) or snag (1), $\text{slp}$ = slope, $\text{est}$ = easting (UTM).

distribution with most logs in decay class 3 (46%). Only 5% of logs were standing. The median slope of the terrain was 0.13 (range: 0-2.10).
Figure 3.5: The probability that a log located in one 6.25 ha plot is occupied by *O. disjunctus* was dependent on a) the size of the log, b) average decay state, c) proximity to conspecifics. These variables were deemed informative based on AICc scores of candidate models. Values are back-transformed model-averaged estimates of least squares means and SE. In order to make graphs most representative, estimates are those predicted when all other predictors are at moderate values (sz = 4.83 territories, dec = 3, Ci= 1.77, sng = downed (not pictured), slope (not pictured) = 0, easting (not pictured) = 0. % $R^2_n$ is the percent of Nagelkerke’s pseudo-$R^2$ explained by a predictor.

is consistent with my hypothesis that the dispersal neighborhood for *O. disjunctus* was on the order of meters. The estimate for conspecific proximity (based on a 3.9 m dispersal neighborhood discussed in the previous paragraph) was a more important predictor of *O. disjunctus* incidence than log proximity (with a 15.5 m dispersal neighborhood; $\sum w_{C3.9} = 1.0$ vs. $\sum w_{H15.5} = 0.1$; conspecific $iR^2_N = 5.0\%$ vs. log $iR^2_N = 2.5\%$; conspecific $\hat{z} = 0.63$ vs log $\hat{z} = 0.01$; Table 3.4). Logs with the highest density of nearby occupied logs (conspecific proximity index = 47.6) were 34.3X (CI = 17.3-66.86) more likely to house *O. disjunctus* than the most isolated logs (conspecific proximity index = 0.0, Figure 3.4). Log size was by far the strongest predictor of *O. disjunctus* incidence in Port Hudson (independently accounted for 25.1% of the variance, Table 3.4, Figure 3.5). The probability that a log contained *O. disjunctus* increased
3.3X (CI = 2.6-4.2) with each 2.7 fold increase in the number of 31.42 dm² log-sections in a log (Figure 3.5). The smallest occupied log had a 26.0 dm² surface area, the same size as my large experimental logs and just under my unit measurement for log-sections (1 section = 31.4 dm²). Decay was also a strong predictor of patch incidence. Logs of moderate decay (decay = 3) were 12X more likely than logs with only incipient decay (decay = 1.5) and were 2.5X more likely than logs in advanced decay (decay = 4.0) to contain *O. disjunctus* (Figure 3.4). Snags were 0.3X (CI = 0.1 – 0.8) less likely to contain *O. disjunctus* than downed logs (Table 3.4, Figure 3.5). Slope of the landscape and x-coordinates were mildly informative (∑w_i < 0.5) such that logs on flat ground and those in the eastern portion of the plot were slightly more likely to contain *O. disjunctus* than those on slopes or in the western side. Y-coordinates were not included in the best set of models.

**Response Range Experiment**

Beetles moved toward logs one meter away more frequently than expected by chance (6/14 beetles > 8.33%; Exact binomial test: *P* = 0.0006), but did not move toward logs three meters away (0/14 ≈ 4.44%, Exact binomial test: *P* = 1.0).

**Habitat Selection and Movement Experiment**

Emigration was positively influenced by log size and the presence of a single *O. disjunctus* pair. Most beetles (87.0%, CI = 77.7-92.7%) left the log in which I placed them. The probability of emigrating was 20% (CI = -50%-+20%) lower when the log was large, and increased when conspecifics were present (one couple: 1.3X, CI = 0.9 – 1.7; >2 beetles: 1.13, CI = 0.89 – 1.42, Table 3.5). Although informative as measured by the reduction in model AIC_c values (Table 3.5), the estimates for the effect of log attributes on emigration were imprecise.
Furthermore, the best models predicting emigration did not provide a high goodness of fit (max $R^2_N = 4.6\%$, Table 3.5).

The probability of an immigrant settling in a small empty log was almost zero (0.07, CI = 0.03 – 0.16, Table 3.6, Figure 3.6), but the odds increased by 13.0X if the log was large (CI = 4.9 – 34.6), and by an additional 2.6X (CI = 1.1 – 6.1X) if the log was originally inhabited by a beetle couple. Logs originally inhabited by a single beetle had an influence intermediate to empty logs and logs with one couple (1.4X, CI = 0.8-2.6) and logs with more than one beetle couple were similar to empty logs in their attractiveness (1.1X, CI = 0.5 – 1.5, Table 3.6, Figure 3.6). The best models of immigration provided a much better fit than models of emigration (max $R^2_N = 36.3\%$, Table 3.6).

Table 3.5 Effect of habitat and conspecific cues on the proportion of beetles emigrating from a log (n = 96 logs).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\bar{x}$</th>
<th>$\hat{z}$</th>
<th>$\sum w_i$</th>
<th>$iR^2_n$</th>
<th>$jR^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Proportion of original beetles that emigrated</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>1.90 (0.33)</td>
<td>-0.27 (0.21)</td>
<td>0.35</td>
<td>0.39</td>
<td>2.7%</td>
</tr>
<tr>
<td>$\beta_{dia}$</td>
<td>2</td>
<td>0.23 (0.17)</td>
<td>-0.03</td>
<td>0.21</td>
<td>4.0%</td>
</tr>
<tr>
<td>$\beta_{N0}$</td>
<td>$\geq 3$</td>
<td>0.12 (0.12)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>b) Best model set</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>intercept only</td>
<td>1</td>
<td>0.00</td>
<td>0.40</td>
<td>0.0%</td>
<td></td>
</tr>
<tr>
<td>dia</td>
<td>2</td>
<td>0.08</td>
<td>0.39</td>
<td>3.2%</td>
<td></td>
</tr>
<tr>
<td>N0</td>
<td>3</td>
<td>1.26</td>
<td>0.21</td>
<td>4.6%</td>
<td></td>
</tr>
</tbody>
</table>

$x =$model-averaged regression coefficients (SE), $\hat{z}$ =standardized regression coefficients , $\sum w_i =$summed Akaike weight, $iR^2_n =$proportion of pseudo-$R^2$ independently explained by a variable in full model, $jR^2_n =$proportion of pseudo-$R^2$ jointly explained with other variables in full model (negative values indicate suppression), $k =$number of parameters in model, $\Delta AIC_c =$change in Akaike information criterion adjusted for small sample sizes, $w_i =$Akaike weight indicating probability that a model is the “true” one, $R^2_N =$Nagelkerke pseudo-$R^2$; $dia =$small (0) or large (1) log, $N0 =$no. original beetles.

(i.e., large standard error). Furthermore, the best models predicting emigration did not provide a high goodness of fit (max $R^2_N = 4.6\%$, Table 3.5).
When beetles were present in the log at the end of the experiment, the number was consistently one or two beetles regardless of log size or the number of beetles originally present (1.80, CI = 1.48 – 2.19, results of Poisson regression in which log size and number of original occupants were uninformative). When two beetles were settled in a log, they were likely to be a male-female pair (25/26, Exact binomial test: P << 0.001). When only one beetle was settled in a log, it was likely to be male (16/20, Exact binomial test: P = 0.012). Thirty-two percent of beetles found in logs after one week were not experimental beetles, but were naturally dispersing beetles from the surrounding forest.

For the 60 beetles that were recaptured in logs, dispersal distances were best described by a power distribution (Figure 3.7). Most recaptured beetles (83%) were caught in or very near
Table 3.6 Effect of habitat and conspecific cues on the probability that one or more beetles immigrated into a log (n = 143 logs).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\beta_0$</th>
<th>$\beta_{dia}$</th>
<th>$\beta_{N0}$</th>
<th>$\beta_N$</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>-2.60 (0.49)</td>
<td>2.56 (0.29)</td>
<td>0.36 (0.29)</td>
<td>0.96 (0.44)</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>0.36 (0.29)</td>
<td>0.18</td>
<td>0.33</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.96 (0.44)</td>
<td>0.55</td>
<td>0.07 (0.38)</td>
</tr>
<tr>
<td></td>
<td>$\geq 3$</td>
<td>0.07 (0.38)</td>
<td>0.02</td>
<td>0.55</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Model</th>
<th>$k$</th>
<th>$\Delta AIC_c$</th>
<th>$w_i$</th>
<th>$R^2_i$</th>
<th>$AUC$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$dia + N0$</td>
<td>5</td>
<td>0.00</td>
<td>0.55</td>
<td>36.3%</td>
<td>0.81</td>
</tr>
<tr>
<td>$dia$</td>
<td>2</td>
<td>0.38</td>
<td>0.45</td>
<td>31.3%</td>
<td>0.76</td>
</tr>
</tbody>
</table>

$x$ = model-averaged regression coefficients (SE), $\hat{z}$ = standardized regression coefficients, $\sum w_i$ = summed Akaike weight, $iR^2_n$ = proportion of pseudo-$R^2$ independently explained by a variable in full model, $jR^2_n$ = proportion of pseudo-$R^2$ jointly explained with other variables in full model (negative values indicate suppression), $k$ number of parameters in model, $\Delta AIC_c$ change in Akaike information criterion adjusted for small sample sizes, $w_i$ Akaike weight indicating probability that a model is the “true” one, $R^2_i$ Nagelkerke pseudo-$R^2$; $dia$ = small (0) or large (1) log, $N0$ = no. original beetles.

Figure 3.7 Distribution of dispersal distances observed for beetles released in experimental 36 X 36 m landscapes. Density is weighted by the number of traps available at each distance for each beetle (depending on where it was released). Linear equations are ordinary least squares models describing the relationship between distance ($x$) and density of beetles ($y$). Two models were compared: an exponential distribution (open circles) and a power distribution (filled circles). Bars indicate observed values. Note the ln-scale on the $y$-axis.
their original log (0-5 m distance class), and another 9% were caught in one of the nearest neighbors (5-10 m distance class).

Performance Experiment

Beetle finite rate of increase was higher in large compared to small logs but was negatively related to conspecific density (Figure 3.8). The number of adults in small logs with one original female increased by 41.36% over the course of the experiment (CI = -19.79% - +231.23% over 157 days). Both log size and the number of females were informative predictors of the proportional change in the number of adults (positively and negatively, respectively), but only populations in large logs consisting of one original female had a growth rate that was significantly greater than 1 (total $R^2_N = 52.9\%$; $iR^2_n$: log size = 16.0\%, no. females = 36.9\%;

Figure 3.8 The influence of log diameter and conspecific density on finite population growth rate from June to November 2008 (n = 28 logs). Values are back-transformed model-averaged estimates of least squares means with standard error bars. Variables are those deemed informative based on the AICc values of candidate models. Different letters indicate significant least squares differences among model-averaged means ($\alpha = 0.05$).
Figure 3.8). The higher finite rate of increase in large logs with fewer females was associated with increased fecundity, juvenile survival, and adult survival (Appendix 2).

**DISCUSSION**

This study demonstrates the potential for sophisticated multi-scale observations of incidence, combined with mechanistic experiments, to make strong inferences regarding the environmental variables and mechanisms underlying distribution. Considering its low mobility, *O. disjunctus* exhibits surprisingly low sensitivity to forest cover in the surrounding landscape. Distribution within the Mississippi river alluvial floodplain is instead most strongly predicted by fine-scale environmental variables (decay state and log-size), as well as flood disturbance at the plot level. Furthermore, although dispersal limitation has been hypothesized to result in strong autocorrelation in distribution, *O. disjunctus* exhibits little residual autocorrelation at all observed levels. These findings are intriguing because dispersal limitation is generally the first attribute of an organism to be considered when attempting to interpret the scale at which an organism responds to its environment (Holling 1992, Holland et al. 2004) or shows variability in abundance (Johnson et al. 2001, Burrows et al. 2009). Although dispersal undoubtedly influences the distribution of *O. disjunctus*, this study emphasizes that the scale at which an organism responds to its environment may be determined more by fine-scale behaviors and response to environmental filters than dispersal limitation.

**Variation in Incidence across Spatial Scales**

Environmental factors occurring at the finest spatial scales were most important when predicting *O. disjunctus* incidence. That the relative importance of both decay and log size to incidence was greater than the importance of the large environmental disturbance incurred by seasonal flooding with multiple meters of water emphasizes the strength of these fine-scale
environmental filters. Variation across scales is not well-studied for terrestrial taxa, but among many marine benthic organisms most of the variation in distribution occurs at fine-scales (reviewed in Fraschetti et al. 2005). Cushman and McGarigal (2004) suggested that deterministic processes might be greatest at the scales within the response range of an organism. Indeed, the scales at which environmental variables exhibited the greatest association with _O. disjunctus_ incidence in my multi-scale survey (logs and log-sections) coincide with the response range of _O. disjunctus_ (between 1 and 3 m) and smaller than the spatial scale at which dispersal limitation is expected to occur (average dispersal distance was less than 10 m). Species traits may influence the spatial scale at which a species exhibits greatest variation in distribution. Strong dispersal ability (Johnson et al. 2001), low trophic level, and moderate proportional incidence (Burrows et al. 2009) have been associated with peaks in variation at larger spatial scales in marine environments.

Although some have hypothesized that strong variation in density across sampling sites will result from limited dispersal (Taylor et al. 1983), _O. disjunctus_ exhibits surprisingly little patchiness in incidence (as measured by the intra-class correlation) suggesting that autocorrelation in incidence is smoothed out by either a) infrequent long-distance dispersal and/or b) the cumulative effect of frequent short-distance dispersal events among nearby logs. The autocorrelation that does exist is strongest at the subplot level, a pattern consistent with the hypothesis that autocorrelation is associated with dispersal distance (dispersal was usually less than 5-10 meters; subplots were separated by >16 m). Five to ten meters represent a small dispersal neighborhood relative to many saproxylic insects which rely on flight (Jonsson 2003, a few km, Brunet and Isacsson 2009), but is similar to the dispersal distances of primarily cursorial beetles such as woodland specialist carabid beetles (<2 m per day, Brouwers and Newton 2009),
Eleodes spp. (Tenebrionidae) (< 50 m, Crist and Wiens 1995), Osmoderma eremita Scopoli (Scarabaeidae) (< 50 m, Ranius 2006), Bolitotherus cornutus Panzer (Tenebrionidae) (Whitlock 1992, < 50 m, Starzomski and Bondrup-Nielsen 2002), and other members of Passalidae (e.g., Spasalus crenatus MacLeay moved an average of 2-6 m, Galindo-Cardona et al. 2007).

Aggregation within logs was almost as great as aggregation within subplots. The redistribution kernel of O. disjunctus which indicates a tendency to disperse less than 10 m suggests that dispersal among logs is probably not strongly limiting (median nearest neighbor distance = 2.8 m). Therefore, this aggregation is most likely caused by something other than dispersal such as conspecific interactions or environmental variables not considered in this study. Two obvious unidentified environmental variables are tree and wood-decaying fungal species. Like many mid- to late-decay associated saproxylic beetles (Wu et al. 2008), O. disjunctus does not appear to perform better on any particular hardwood taxon (Gray 1946), nor is there a clear association with a particular type of white rot (the fungal functional guild most commonly found in hardwoods, Liese 1970). One other factor that many saproxylic insects are sensitive to is insolation (Chen et al. 2002, Buse et al. 2007, Brunet and Isacsson 2009). The fact that O. disjunctus is positively associated with decreased canopy cover at the subplot level suggests that it may also benefit from increased insolation.

The influence of conspecific interactions on patterns of O. disjunctus incidence is complex. O. disjunctus was more likely to settle in an experimental log that was or had been recently occupied by conspecifics (my sampling could not distinguish between the two options), but emigration of conspecifics prevented aggregation from occurring. One or more of the original occupants either left before the new immigrant arrived or was displaced by an immigrant. This tendency not to aggregate within the experimental logs in spite of attraction to
conspecifics during dispersal was important because when otherwise forced to live together in
the same logs in performance experiments, *O. disjunctus* experienced decreased fitness in the
presence of conspecifics. These results suggest that conspecifics may benefit dispersers by
guiding them to habitat, as do conspecifics of the forest bat *Nyctalus noctula* (Ruczynski et al.
2007), by providing dispersers with a proximate cue of habitat quality (e.g., *Anolis* lizards,
Stamps 1987), or by guiding immigrants to potential mates (e.g., bark beetle *Ips subelongatus*,
Zhange et al. 2007). These data cannot distinguish among these three ultimate causes for
conspecific attraction. However, a post-dispersal benefit to conspecifics (e.g., enhanced
protection from predators, Nelson and Jackson 2008), can be ruled out as an ultimate cause for
attraction because of the clear negative influence *O. disjunctus* conspecifics had on fitness. It is
important to note that my performance experiments indicated that the experimental logs used in
these experiments were just large enough for a single beetle pair to experience positive fitness.
Based on the short redistribution distances of beetles, I hypothesize that were logs larger,
aggregation associated with conspecific attraction during search and settlement would occur
because immigrants or displaced residents would be likely to settle close to the original territory.
Consistent with this hypothesis are simulation and empirical experiments with birds which
indicate that greater density in large patches can result from conspecific attraction (Fletcher

I expect that had my survey extended to areas outside of the Mississippi river valley that
variation in incidence at the plot level would have been greater because of potential effects of
slower decay schedules (due to decreased moisture), altered CWD input schedules (due to
reduced hurricane damage in areas further from the coast), and increased proportion of
uninhabitable softwoods in upland areas to name a few potential sources of large-scale variation.
Although many studies document that the scale at which species respond to the
surrounding landscape varies widely among species (birds: 2-2827 ha, Mitchell et al. 2001,
cerambycid beetles: 20 - 2000 meters, Holland et al. 2004, parasitoid wasps: 0.2 - 7.0 km, Gibb
et al. 2008), a general explanation for patterns in the spatial scale of response to landscape
context is lacking. Body size (Roland and Taylor 1997, Holland et al. 2005) and habitat
arrangement (Woolnough et al. 2009) have been implicated. A study of thirty-one cerambycid
(also saproxylic) beetle species (Holland et al. 2005) showed that scale of response to forest
cover increased with body size, such that the smallest (5 mm) and largest (23.5 mm) cerambycid
species in the study were expected to respond to forest cover at the 1.4 ha scale (∼66 m radius)
and the 1600 ha scale (∼2 km radius), respectively. Although 50% larger (32 mm), O. disjunctus
had a much smaller scale of response (225 ha, ∼0.75 km radius) than the largest cerambycid in
their study. If the link between body size and scale of response to habitat abundance is associated
with step-lengths (distance between each move) during dispersal (as suggested by Holling 1992),
then this disparity might be explained by the difference in cerambycid and passalid dispersal
mode: cerambycids rely on flight and O. disjunctus is primarily cursorial.

Environmental Filters

Environmental filters are often the first factors considered when explaining the
distribution of a population (Hutchinson 1957, Fretwell 1972). The habitat associations of a
species are a powerful indicator of its evolutionary history (Wiens and Graham 2005) and can be
used to predict its population trajectory in the presence of anthropogenic change (Pearson and
Dawson 2003).

Decay class – a variable associated with remaining patch life (Zell et al. 2009) and
nutritional quality (Clinton et al. 2009) – was the most important factor associated with O.
disjunctus incidence. Saproxylic insects in general are sensitive to decay class. More than log diameter, decay class is associated with dramatic turnover in beetle species composition (reviewed in Grove 2002). In artificial diet experiments, O.disjunctus avoided foods containing lignin (M. Blackwell and S. Gross, personal communication), a sugar that is broken down during early decay stages by white-rot fungi (Hatakka 1994), suggesting that lignin might be a substance preventing O. disjunctus from inhabiting early decay wood.

The pattern of greater incidence of O. disjunctus in large logs is consistent with incidence patterns of numerous other saproxylic species. Large diameter logs are associated with greater species richness and are more likely to house rare or threatened species (reviewed in Grove 2002; but see Ferro et al. 2009). My performance experiment indicates that O. disjunctus population growth rate is negative below a certain log size (28 dm² surface area), suggesting that space limitation is an important factor limiting incidence in small logs. Large logs may provide advantages beyond meeting minimum space requirements; thicker walls in large logs provide improved microclimate stability, and large diameter is associated with longer persistence times (Harmon et al. 1986, Zell et al. 2009). Furthermore, decay properties are highly variable within logs (Saint-Germain et al. 2010), especially large ones (Allen et al. 2000), and therefore an individual might expect new habitat to become available in future breeding seasons (Arlt and Part 2007). My settlement experiments further showed that beetles actively preferred large logs during settlement, potentially helping to explain the positive incidence-area relationship observed in my surveys. This active preference for a large log is interesting because most explanations of density-area relationships do not consider the possibility that patch size itself is an important cue for settlers (Bowman et al. 2002, Hambäck and Englund 2005).
Flood history was the strongest predictor of incidence rate at the plot level such that log-sections in regularly flooded areas were less likely to be occupied. Given the regularity and depth of floods in unleveed areas (most years for multiple months), it is surprising that *O. disjunctus* was present in these sites at all. Although it is possible that eggs can survive heavy flooding (as do some carabid eggs, Kleinwachter and Burkel 2008), *O. disjunctus* larvae would be unlikely to survive without parental food provisioning (Pearse et al. 1936). Therefore, the few *O. disjunctus* individuals found in areas prone to heavy flooding are probably the result of adult survival in refugial logs (floating logs or tall snags, e.g., Braccia and Batzer 2001) or recent colonization from outside the flooded area (perhaps through rare flight). Two tropical passalid species survive in heavily flooded areas, probably by limiting reproduction to the dry season (immatures were not observed in the wet season, Mouzinho et al. 2010). Greater sensitivity to flooding than to other major anthropogenic modifications in the area (e.g., forest loss) suggests that *O. disjunctus* may actually benefit from anthropogenic interference in the lower Mississippi river alluvial floodplain. The region is highly modified by an extensive levee system that protects most bottomland areas from major floods (Lambou and Hern 1983).

Of the three major wood-boring groups in the lower Mississippi river alluvial floodplain (termites, other-wood boring beetles, and ants) only ants exhibited a negative relationship with *O. disjunctus* incidence. Which ant taxa might be driving this relationship, and whether this negative association is due to divergent habitat preferences (e.g., ants were more likely to be found in less decayed wood) or direct competition requires further investigation. The presence of other wood-boring beetles (usually cerambycid larvae) was positively associated with *O. disjunctus*, possibly due to similar habitat requirements.
Measures of relative importance are strongly influenced by the range from which samples are drawn. In my study, sampling was restricted to sites with at least a minimal probability of passalid incidence based on prior knowledge. Samples were restricted to forested areas at the landscape scale and to hardwood logs (as opposed to softwood logs or other decayed material such as leaf litter) beyond decay class 1 with diameter greater than 5 cm. Had I conducted unrestricted sampling within the Mississippi river alluvial floodplain, I would expect an increase in the estimated importance of fine-scale environmental filters (decay, diameter, and wood type would be even more important if completely uninhabitable samples had been included) and landscape-level environmental filters (e.g., if non-forested areas were included).

Conclusion

Although sensitivity to large-scale environmental phenomena (e.g., forest loss) is a consistent pattern across taxa (Andren 1994, Fahrig 2002, 2003), this study emphasizes the importance of fine-scale (cm to m) environmental variation in the distribution of *O. disjunctus*. Studies of marine benthic organisms suggest that patchiness at fine-scales may be a general feature across taxa (reviewed in Fraschetti et al. 2005). Therefore, the use of easily measured landscape-level environmental patterns (e.g., habitat abundance) to make predictions about the welfare of populations should be tempered by awareness that their importance is likely a composite of underlying fine-scale processes that may be of greater importance. I suggest that critical management decisions should be informed by explicit consideration of the scale at which the most important patterns in incidence or abundance occur. Non-invasive surveys followed by experiments targeted at a single scale can reduce the sample size required to produce powerful conclusions. Although this study cannot discount the potential explanatory value of large scale features (number of trees, Ranius 2002, e.g., amount of suitable stand type, Gibb et al. 2006,
forest age and area, Irmler et al. 2010), especially in areas such as Europe where large-scale anthropogenic impacts have been more intensive and long-term than in southeastern United States, my study suggests the potential for effective management to focus at small scales to improve the size and quality of wood.

Although low mobility is often associated with vulnerability to large-scale habitat disturbance (Karr 1982, de Vries et al. 1996, Louy et al. 2007, Hendrickx et al. 2009), the distribution of \textit{O. disjunctus} illustrates that dispersal limitation can coincide with a high incidence in the presence of large scale habitat loss (see also Diekötter et al. 2010). My study suggests that for response to patch-size and conspecifics may alter incidence at fine-scales. How these individual-based “informed dispersal” (Clobert et al. 2009) decisions scale up to affect populations is not well-understood, but a few studies have indicated the potential for informed decisions to completely alter large-scale outcomes (Schmidt 2004, Fletcher 2006). Future research can improve my understanding of the interaction between mobility and landscape features by further investigating the large-scale population-level outcomes of fine-scale individual behavior.
Chapter 4: Search Strategies and the Density-Area Relationship

INTRODUCTION

A large body of literature in behavioral ecology documents the ability of organisms to orient toward cues during their search for settlement habitat (e.g., beetles, Jonsell and Nordlander 1995, rodents, Zollner 2000, fish, Mitamura et al. 2005, toads, Sanuy and Joly 2009), but less is known about how information gathered during or before dispersal (i.e., informed dispersal, Clobert et al. 2009) influences population distribution and dynamics (Clobert et al. 2009, Schmidt et al. 2010). Informed dispersal behavior has been shown to strongly influence population level processes (see Schmidt 2004, Duckworth and Badyaev 2007). For example, Fletcher (2006) incorporated orientation toward conspecifics (a common search strategy used by birds, Ward and Schlossberg 2004, Ahlering et al. 2010) in a simulation model of movement and found that densities in large patches were increased relative to densities in small patches, replicating the positive density-area relationship (also called the patch-size effect) widely observed among birds (Bender et al. 1998). Until this study, non-dispersal related mechanisms had been invoked to explain the density-area effect (Bender et al. 1998, Debinski and Holt 2000, Vergara and Hahn 2009). This example illustrates how simulation studies can help bridge the gap between animal behavior and population processes.

The association between density and patch size (called the patch-size effect or the density-area relationship) is an important pattern in theoretical (Hambäck and Englund 2005) and conservation biology (Bender et al. 1998, Bowman et al. 2002). Theory suggests that conspecific attraction is expected to make the density-area relationship more positive (Fletcher 2006) and habitat attraction is expected to result in a negative or null density-area relationship depending on whether habitat attraction is proportional to the perimeter or the area of a patch, respectively
The effect of mate attraction, a common strategy in which an individual is attracted to a member of the opposite sex rather than to habitat per se (Murlis et al. 1992, Hopper and Roush 1993, Jonsson et al. 2003), on the density-area relationship has not been explicitly considered. As a socially based cue, mate search might be expected to result in similar patterns to conspecific search (i.e., disproportionate increase in density with patch-size, Fletcher 2006, 2009). On the other hand, mate attraction could increase residency in small patches relative to random search if mate attraction prevents individuals from leaving a small patch for lack of mating opportunities (Fagan et al. 2010). Given how common the mate search strategy is in nature (Vickers 2000, Belanger and Corkum 2009), its potential to influence the density-area relationship is an important consideration.

The fitness conferred by informed dispersal might be expected to change over time if informed dispersal leads to distribution patterns which alter the usefulness of information. If, for example, conspecific search, which usually benefits individuals by guiding them to habitat, leads to greater aggregation on large patches (Fletcher 2006), then negative-density dependence might eventually select against conspecific search. The negative effect of intraspecific competition on the optimal strength of conspecific attraction could depend on dispersal limitation and/or isolation among patches. If dispersal is limited, then a cue that increases detection of patches may be favored, especially if dispersal limitation prevents densities from reaching high numbers. A long-term study of the feedback between search strategy and population processes over time has not been conducted.

I investigated the potential for fine-scale habitat search behaviors to explain the strong positive relationship between the area and the density of occupied territories observed for a saproxylic (=decayed-wood dependent) beetle, *Odontotaenius disjunctus* Illiger (Coleoptera:
Passalidae). I developed a spatially explicit, multi-generation, individual-based simulation model which replicates movement, reproduction, and mortality of *O. disjunctus* and the spatial and temporal complexity of the discrete habitat patches (i.e., coarse woody debris) among which it disperses. This study was motivated by my findings that *O. disjunctus* is responsive to habitat, mate, and conspecific cues during habitat settlement (Chapter 3).

For this study, I had three specific goals: 1) to evaluate the long-term population consequences of informed dispersal based on three different cues (habitat, mate, or conspecific density) with a particular emphasis on their contribution to the density-area relationship; 2) to predict the optimal strength of cue-response in relation to dispersal limitation; and 3) to investigate the interacting effects of search strategy and dispersal limitation on individual fitness. Animals frequently respond to habitat (Belanger and Willis 1996, Zollner and Lima 1997, Schooley and Wiens 2003), mate (Murlis et al. 1992, Gerhardt 1994), and conspecific (Ward and Schlossberg 2004, Fletcher and Sieving 2010) cues, but the consequences of these search strategies for populations are not well-explored. I tested the effectiveness of each search strategy over a range of dispersal limitation (time to starvation = 14, 7, or 4 days) in order to evaluate the ability of a search strategy to compensate for loss of mobility. To my knowledge, this study is the first to investigate the effect of mate search on the density-area relationship. Furthermore, although the effects of habitat and conspecific attraction on the density-area relationship have been investigated (Schtickzelle and Baguette 2003, Fletcher 2006), the optimal responsiveness to habitat and conspecific cues over a long period of time has not.

Although I expect my insights concerning the relationship between search strategies and the density-area relationship to have implications for most animals with time limited dispersal, I parameterized this model with dispersal and distributional data from my extensive work with *O.*
O. disjunctus (Jackson et al. 2009, Chapter 3). An important goal for this model, therefore, is an understanding of the potential for informed dispersal observed at fine-scales to explain the large-scale distribution of O. disjunctus.

METHODS

Study System

O. disjunctus is a large beetle (~32 mm from tip of horn to apex of abdomen) whose range covers eastern North America from Florida to southern Ontario, and from Kansas to the east coast (Schuster 1978). Socially monogamous O. disjunctus couples create extensive galleries in wood in which they care for their offspring into adulthood (Schuster and Schuster 1985), a process that takes about three months during the summer (in North Carolina, Gray 1946). During this time they are seldom found outside of their log (in Louisiana, Jackson et al. 2009), and presumably leave the log later only to find new breeding territory. O. disjunctus is highly territorial (Gray 1946, Schuster 1975a) and generally avoids densities of greater than one pair per 30 dm² log surface area (Chapter 3). The process of mate and habitat location is not well-understood, but some evidence suggests that one beetle, either male or female, initiates a gallery and is joined by a mate within a few days (Schuster 1975a). Rare flight has been documented (Hunter and Jump 1964, MacGown and MacGown 1996), but the vast majority of movements are cursorial (Jackson et al. 2009). Movement is especially slow in non-forest habitat, indicating that beetles are poorly suited to movements outside of the forest. Furthermore, O. disjunctus exhibits a strong reflection response to forest boundaries suggesting that it is attracted to forest and are unlikely to emigrate from forested areas (Jackson et al. 2009). O. disjunctus exhibits high incidence within and among forests, and its incidence is surprisingly insensitive to variation in forest or coarse woody debris abundance (Chapter 3), even though O.
disjunctus is characterized by low mobility (Jackson et al. 2009) and decreased habitat is expected to increase distance among habitat patches. Lifespan of O. disjunctus is unknown, but is probably between 2 and 4 years (Gray 1946, Schuster and Schuster 1997), which encompasses 2-4 breeding seasons.

In a habitat settlement experiment, O. disjunctus was 10 and 4 times more likely to visit a log if it contained a potential mate or was large, respectively (H.B.J., unpublished data). The final location of beetles was also positively affected by conspecifics: beetles were more likely to immigrate into 27.7 dm² logs containing conspecific pairs (Chapter 3). The size of the log, however, was the strongest predictor of increased immigration (Chapter 3). These experiments show that O. disjunctus is sensitive to the cues investigated in this study (habitat, mate and conspecific cues). Here I investigate each of these cues separately to understand their potential effect on large scale distribution.

Model Description

The model description follows the ODD (Overview, Design concepts, and Details) protocol for describing individual-based models (Grimm et al. 2006).

State Variables

For this model I envisioned a landscape comprised of three basic units: patches which were subdivided into territories and were inhabited by individuals. This concept of the patch as an aggregation of territories is appropriate for many animal species which divide resources among territories with discrete boundaries (e.g., speckled wood butterfly, Pararge aegeria, Davies 1978, coral-reef fish, Thalassoma bifasciatum, Warner and Hoffman 1980, tropical arboreal ants, Davidson 1997, ovenbirds, Seiurus aurocapillus, Burke and Nol 1998, wolves, Canis lupus, Corsi et al. 1999, ring-tailed lemurs, Lemur catta, Cavigeli and Pereira 2000,
collared lizards, *Crotaphytus collaris*, Baird and Curtis 2010). Specific to my model was the representation of a patch as a linear series of *O. disjunctus* territories (also referred to in this text as log-sections). My representation of logs, log-sections, and individuals is briefly described here, but the processes in which they are involved (physical environment, decay, dispersal, reproduction, and mortality) are described in more detail in “Submodels”.

Similar to patches in other patch networks (patches of disturbed forest, for example, Mladenoff et al. 1993, Honnay et al. 1999), logs in the model a) were predominantly small, b) were aggregated at small scales, c) varied in age, and d) varied in quality according to a successional pattern. At tree death, each log was assigned a continuous x,y location of the log center, center diameter, a number of territories, a direction from its large end to its small end, an age, and decay parameters (see “Physical Environment” and “Decay” submodels).

Each log-section had the same surface area (27.7 dm²), but unique x,y coordinates, diameter, length, and decay parameters (see “Physical Environment” and “Decay” submodels). Log-sections were either suitable or unsuitable for habitation by beetles, a classification which was dependent on decay state (suitable was defined as moderately decayed, =decay classes 3 and 4, see Pyle and Brown 1998 for description of decay stages) and which dictated whether a beetle could settle or not. An abrupt shift between suitable and unsuitable log conditions was modeled for the sake of simplicity; in reality, the change in log suitability is presumably gradual and predictable to *O. disjunctus*, a situation which may lead to interesting information-based changes in allocation to reproduction and dispersal (much like reproduction/dispersal tradeoffs in plants over successional gradients, Ronce et al. 2005) that require further investigation. In my model, suitable log-sections were equal in quality (i.e., same fecundity and mortality rates), and therefore varied only in their spatial attributes (i.e., proximity to other territories). Settlement in a
territory was important for model beetles because settlement prevented starvation (*O. disjunctus*' only food source is woody material, Pearse 1936), was associated with a lower daily mortality rate (dispersal for many animals is associated with greater predation risk, e.g., Yoder et al. 2004), and allowed an individual to mate (*O. disjunctus* nests within logs, Schuster and Schuster 1985).

Traits of individual beetles were tracked from egg to death. Traits which remained constant from birth included sex (male or female, 1:1 sex ratio), genetically determined cue-responsiveness, and expected fecundity (expected fecundity varied by beetle as described in the “Reproduction” section).

In Experiment One, I tested the effect of evolved cue-responsiveness on the density-area relationship. Cue-responsiveness was a quantitative trait which determined how strongly a beetle oriented toward cues (habitat, mate, or conspecific density, depending on the treatment) during dispersal (Table 4.1, described further in “Dispersal” section). The main goal of the genetic component of this model was to provide a mechanism for optimal cue-responsiveness to evolve; the specific model of inheritance (single-locus quantitative trait based on a diversity of alleles) was selected because it was simple (one locus) and yet allowed for a continuum of cue-responsiveness, but is not meant to represent the true system of inheritance for cue-responsiveness which is not well-studied, but probably involves more than one locus (see studies of fly and moth olfactory responses, e.g., Syed et al. 2006). In Experiment Two, I compared the fitness value of cue-responsiveness with random search. Cue-responsiveness was set to a fixed value for all individuals and a second trait, unresponsiveness to cues, was added to act as a regulatory gene that could “turn off” cue responsiveness and limit an individual to random search behavior.
Throughout its life, a beetle’s age, stage (juvenile or adult), and dispersal stage (dispersing, temporarily-settled, permanently-settled) were monitored. A pattern of visiting multiple sites (temporary settlement) before settling with a mate (permanent settlement) is consistent with observations of high turnover in experimental logs before *O. disjunctus* adults paired and began building substantial galleries together (Chapter 3, see Jonsson et al. 2003 for another model which includes mating-dependent sequential settlement). Multiple temporary visits to habitat before permanent settlement is described for other dispersers (e.g., brush mice, Mabry and Stamps 2008, flying squirrels, Selonen and Hanski 2010), and may indicate choosiness (e.g., Mabry and Stamps 2008), continued search for a mate (as modeled by Jonsson et al. 2003), temporary foraging (thereby increasing chances of dispersal success, Zollner and Lima 2005), or expulsion by conspecifics (e.g., Cutts et al. 1999).

In the model, dispersing was a high-risk state with an increased daily mortality rate and a time limit which, if exceeded, resulted in death by starvation. Many models of dispersal among patchily distributed habitat assume that risk of starvation or energy depletion is an important feature of dispersal (e.g., Stamps et al. 2005, Zollner and Lima 2005).

Dispersal ended with temporary-settlement in my model, a state in which beetles could mate if a mate was in the same log-section; otherwise the beetle might disperse again. Permanent settlement was the result of mating, and permanent settlers could not disperse again. If, however, a beetle became widowed and childless, its condition changed from permanently settled to temporarily settled at which point dispersal was an option. This concept of permanent settlement is based on my observation that *O. disjunctus* is highly unlikely to be caught dispersing during the active breeding season (Chapter 2), and both parents invest in offspring care until offspring reach adulthood (Schuster and Schuster 1985). A similar annual cycle (mobile mate and habitat
selection period followed by a sedentary territorial breeding period) is common for other animals with parental care such as many birds (Gill 1995), some mammals (Gaines and McClenaghan 1980), and numerous sub-social and social insects (Tallamy and Wood 1986).

Dispersal related traits of beetles which were tracked in the model included location (grid-cell and x,y location), net displacement from natal habitat, number of dispersal events, and time since dispersal was initiated.

**Aggregate Variables**

Aggregate variables (those variables which summarize basic units) tracked at the log-section level included the number of unmated adult males and females and an indicator (presence/absence) of permanently-settled adults. Aggregate variables tracked by cell included the number of suitable sections, the number of sections occupied by unmated males and females, and the number of sections occupied by mated pairs. At the landscape-level, the total number of live adults, suitable sections, and occupied sections were tracked. Lastly, I monitored the mean genotypic value for cue-responsiveness (Table 4.1, see “Dispersal” below).

**Table 4.1 Search strategies used to determine movement direction.**

<table>
<thead>
<tr>
<th>Search strategy</th>
<th>Movement rules</th>
<th>Attractant (monitored by cell)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Random search</td>
<td>Correlated random walk(^1)</td>
<td>No attractants</td>
</tr>
<tr>
<td>Informed dispersal</td>
<td>Correlated random walk, but if attractants are within perceptual range, then orientation is biased in direction of attractants. The strength of the bias is determined by the genotypic value for informed dispersal (see Table 4.4).(^2)</td>
<td>Habitat search (Number of suitable territories)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Mate search (Number of potential mates temporarily settled in suitable territories)</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Conspecific search (Number of conspecific pairs permanently settled in suitable territories)</td>
</tr>
</tbody>
</table>

Source: 1) Turchin (1998), 2) Fletcher 2006
Figure 4.1 Flow chart of *O. disjunctus* model. Rectangular boxes indicate processes and diamond-shaped boxes indicate the units by which a loop was counted.
**Process Overview and Scheduling**

This model simulated the yearly decay of logs and the daily movement, reproduction, and mortality of *O. disjunctus* on 513 X 513 m maps of 1 m² cells (Figure 4.1). This landscape size was selected because it allowed for large but computationally manageable numbers of beetles (~11,000 beetles in medium dispersal limitation treatments), thereby avoiding frequent extinction and genetic drift. The odd number of cells (513X513) is an artifact of the midpoint displacement algorithm (Saupe 1988) which I used to generate random landscapes (see “Physical Environment”). Logs were distributed across the landscape in continuous space, each consisting of a series of 27.7 dm² surface area sections (the area associated with positive growth rate for *O. disjunctus*, Chapter 3). I envisioned each log to be a patch and each log-section to be a territory (Kareiva 1985 used a similar concept when he considered a patch to be an aggregation of collards). Decay was updated yearly and new logs were added to maintain a constant number of territories (Figure 4.1). Adult beetles were classified according to one of three dispersal classes: dispersing, temporarily-settled or permanently-settled. The dispersal phase began with a decision to disperse, and only temporarily-settled adults had the option of dispersing (probability assessed daily). Although research with other animals indicates that the tendency to disperse is sometimes different for natal (= first-time) vs. breeding dispersers (Greenwood and Harvey 1982, Wauters and Dhondt 1993, Paradis et al. 1998), no evidence for dispersal differences among *O. disjunctus* age-classes exists (Chapter 2, H.B.J., unpublished data) and differences were not modeled. Dispersal can be divided into smaller time steps which effectively capture the shape (turning angles, step-lengths) of dispersal paths (Turchin 1998). For *O. disjunctus* a two minute time step for 30 steps a day resulted in 0.5-1.5 m step lengths (about the scale of *O. disjunctus* perceptual range, Chapter 3) and one hour of movement per day (the average time naturally dispersing
beetles moved in a field study, Chapter 2). Like many animals (Kareiva and Shigesada 1983),
model beetles moved according to a correlated random walk (parameterized by observations of
naturally dispersing beetles, Jackson et al. 2009; see Turchin 1998 for more information about
correlated random walks) except when movement direction was biased by attractants within its
perceptual range (see “Dispersal”). In the presence of attractants, movement direction was a
weighted average of the correlated random walk direction and the average direction of attractants
(“Dispersal”, Table 4.1). At each dispersal step, a random number was drawn to determine which
(if any) of the log-sections in the current cell a beetle would temporarily settle in (temporary
because settlement was not permanent until mating occurred). Dispersal ended when a beetle
became temporarily-settled in a log-section. To account for the risks of prolonged dispersal
(energy-depletion and increased mortality, e.g., Johnson et al. 2009), dispersers which had not
temporarily-settled within four, seven, or fourteen days of initiating dispersal (depending on the
dispersal limitation treatment) died of starvation (starvation times based on laboratory starvation
However, dispersers that found temporary settlement had their energy restored completely. The
immediate renewal of energy reserves is a simplification of a process that would take longer
(days in Drosophila, Roff 1977) in nature. Temporary-settlement lasted until a) a beetle mated
and became permanently settled or b) a beetle dispersed again. Permanent settlement lasted until
a beetle became both widowed and childless at which point its status was returned to
temporarily-settled, thereby giving it the option to disperse. Mated females had a daily fixed
probability of producing an egg each day during the breeding season (May 1 to June 20 in my
model, similar to observations of O. disjunctus in North Carolina, Gray 1946), which resulted in
asynchronous maturation of juveniles (asynchronous hatching is also common for birds, Clark
and Wilson 1981). Juveniles matured 110 days after birth to become temporarily-settled adults (Gray 1946). Fixed mortality rate was greater for juveniles than adults, and was greater during dispersal than during temporary or permanent settlement. The maximum adult age was capped at four years, the maximum life-span expected for *O. disjunctus* (Gray 1946, Clark and Wilson 1981, Schuster and Schuster 1997).

**Design Concepts**

Emergence (patterns which are not imposed by but result from the model): Distribution-related parameters emergent in this model include overall beetle incidence, the density-area relationship and its components: immigration-area and emigration-area relationships. The average strength of cue-responsiveness was emergent from the model. The performance of individuals in terms of fitness, survival, mating success, time spent dispersing, number of dispersal events, and net displacement were also emergent. Sensing: Depending on the search strategy treatment, beetles had the ability to sense and orient toward habitat, mates, or conspecifics from one cell away during dispersal. Conspecific interactions: Mating of two beetles temporarily-settled in the same section was explicitly modeled. Dispersal and settlement is density-dependent for many animals (Bowler and Benton 2005). In my model, density-dependence was incorporated in two ways: if a mating pair occupied a section, the probability of immigration into the section was 0 and the probability of emigration for any temporarily-settled beetles in the section was 1. This behavior is consistent with territorial behavior observed in *O. disjunctus* (Valenzuela-González 1986, Wicknick and Miskelly 2009) and the territorial spacing (one beetle couple per 27.7 dm² surface area) observed in a habitat settlement experiment (Chapter 3). Second, pre-emptive site selection had the effect of making dispersal time and dispersal-related mortality positively density-dependent at the population level. Stochasticity:
Most demographic and behavioral parameters were drawn from probability distributions (usually empirically based) in order for the model to better replicate known patterns (see Tables 4.2-4.5).

Initialization

At the beginning of each simulation, beetles were randomly assigned to suitable log-sections as couples with four juvenile offspring (four was the average number of offspring found during a census of *O. disjunctus* nests, Chapter 3). Adults were randomly assigned an age between 434 and 474 days (i.e., they were assumed to have been born in the previous breeding season), and juveniles were randomly assigned an age between 69 and 109 (i.e., born during the current breeding season). The initial occupancy rate was 22% (a similar incidence rate was found in both Mississippi river valley and the Port Hudson surveys, Chapter 3).

Input

The only environmental process external to beetles was the decay of log-sections. Decay state was updated yearly with the result that some log-sections became suitable for settlement and others became unsuitable (resulting in the death of juveniles and emigration of adults). In order to eliminate a potentially distracting cause of demographic fluctuations, the number of log-sections was kept nearly constant with the addition of new logs each year. The number of log-sections was nearly (but not completely) constant because the size of each new log was randomly drawn from a distribution of sizes and could potentially cause the number of log-sections to exceed the yearly limit.

Submodels

Submodels describe the main processes simulated in this model including: physical environment, decay, dispersal, reproduction, and mortality.
### Table 4.2 Parameterization of the physical environment submodel.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Function</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>H</td>
<td>Aggregation of log centers(^1)*</td>
<td>0.0</td>
<td>unitless</td>
</tr>
<tr>
<td>(\sigma)</td>
<td>Standard deviation of log center aggregation(^1)*</td>
<td>1.0</td>
<td>unitless</td>
</tr>
<tr>
<td>(L_{diam})</td>
<td>Diameter of a log(^1)</td>
<td>(\text{Diameter class (Cumulative distribution): 7-10 (0.2973), 10-15 (0.6712), 15-20 (0.8333), 20-25 (0.8919), 25-30 (0.9324), 30-35 (0.9640), 35-40 (0.9775), 40-45 (0.9865), 45-50 (0.9910), 50-55 (0.9955), 55-60 (1.0000)})</td>
<td>cm</td>
</tr>
<tr>
<td>(L_{length})</td>
<td>Length of a log(^1)</td>
<td>(e^{\beta_0 + \beta_1 L_{diam} + \varepsilon}, \text{where } \beta_0 = 2.4220 \text{ and } \beta_1 = 0.5105, \varepsilon \sim N(0.0000, 0.6582))</td>
<td>m</td>
</tr>
<tr>
<td>(L_t)</td>
<td>Number of 27.7 dm(^2) surface area sections in a log</td>
<td>Assuming each log was a cylindrical frustum: (\frac{\pi (r_{lg} + r_{sm})^2}{27.7 \text{dm}^2} \sqrt{(r_{lg} - r_{sm}) + \frac{L_{diam}^2}{2}},) Where (r_{lg}) and (r_{sm}) are the large and small end radii, respectively</td>
<td>unitless</td>
</tr>
<tr>
<td>(L_\alpha)</td>
<td>Direction of log from large end to small end</td>
<td>(U(-2\pi, 2\pi))</td>
<td>radians</td>
</tr>
<tr>
<td>(T_x, T_y)</td>
<td>Section x,y coordinates</td>
<td>(T_{x_i} : L_x - 0.5L_{length} \sin(L_\alpha)), (T_{x_{n-1,i}} : T_{x_{n-1}} + L_{length} \sin(L_\alpha)), (T_{y_i} : L_y - 0.5L_{length} \cos(L_\alpha)), (T_{y_{n-1,i}} : T_{y_{n-1}} + L_{length} \sin(L_\alpha))</td>
<td>m</td>
</tr>
<tr>
<td>(T_{diam})</td>
<td>Section diameter</td>
<td>(T_{diam_i} : \frac{1}{\tan(\theta a)} L_{length} + L_{diam}) (T_{diam_{n-1,i}} : T_{diam_{n-1}} - \frac{1}{\tan(\theta a)} T_{length_{n-1}})</td>
<td>m</td>
</tr>
<tr>
<td>(T_{length})</td>
<td>Section length</td>
<td>(0.277 m^2 \frac{1}{\pi(T_{diam})})</td>
<td>m</td>
</tr>
</tbody>
</table>

\(^1\)calibrated (See “Calibration”); Sources: 1) (Port Hudson Census, census of 666 hardwood logs in mixed hardwood forest near Baton Rouge, LA, Chapter 3); 2) Zell et al. (2009)
In each of the 513 X 513 m landscapes coarse woody debris dynamics were simulated for 50 years in order to achieve a stable age distribution of logs. Beetles were then added and the simulation was run for another 100 years unless otherwise indicated (Figure 4.1).

**Spatial Distribution of Logs**

In order to create a spatial distribution of patches (=logs) similar to that found in natural forests, I used a midpoint displacement algorithm (a commonly used algorithm to generate realistic natural landscapes, Saupe 1988, for examples see Hill and Caswell 1999, With and King 1999) to generate a fractal distribution of values for each 1 m² cell. This algorithm required two input values: H, a value between 0 and 1 (where 1 results in a strongly clustered distribution), and $\sigma$, the initial standard deviation of the zero-centered normal distribution from which each value was drawn. The values for H and $\sigma$ were determined by calibration of simulated landscapes with an empirical landscape (see “Calibration” below). Using the logistic function, each resulting value was transformed into a probability of containing at least one log center. Starting in the bottom left-hand corner of the grid, these probabilities were added to form a cumulative distribution of probabilities. For each log, the location of its center was drawn from this cumulative distribution. Continuous x and y coordinates for the log center were randomly drawn from a uniform random distribution representing the boundaries of that cell.

**Properties of Logs**

Each log was assigned a size. Center diameters ($L_{diam}$) in year 0 were drawn from an empirically-based distribution (strongly right-skewed, Port Hudson Census, Chapter 3, Table 4.2). The rate at which each log diameter class was added to the landscape each year was calibrated to achieve equilibrium in log center diameters (otherwise log diameter unrealistically increased over time with the potential of causing large changes in patch dynamics). Length
(L_{length}) was calculated based on a linear regression model which related length to diameter in an empirical dataset (Port Hudson Census, Chapter 3, Table 4.2). Variation in log-section diameter within each log was modeled by assuming that each log was a conical frustum such that log diameter was assumed to decline at a constant rate from the large to small end. The purpose of incorporating this level of realism into log shape was to allow variation in decay (which is diameter-dependent) to occur within a log for the sake of future investigations into the effect of fine-scale (within-log) habitat preferences based on diameter and decay. The average slant from the large end to the small end of a log the Port Hudson census was 1.56 radians. This angle, along with the length of the log, was used to calculate the large and small end diameters of the log and the resulting surface area of the log. The number of log-sections (L_{t}) in a log was then calculated by dividing the surface area of the log by 27.7 dm². If a log had less than 27.7 dm² surface area, log length was less than 0.5 m, or log center was less than 7 cm in diameter, the log was recalculated and replaced by a new log in a new location. The direction from a log’s large to small end (L_{\alpha}) was drawn from a uniform circular distribution. Each territory within a log was assigned x,y coordinates (T_x,T_y), and diameter (T_{diam}) and length (T_{length}) consistent with its location on the log (Table 4.2).

Decay

Decay determined the percent density remaining in a log-section (and the consequent suitability for \textit{O. disjunctus}) and was updated at the end of each year. Decay of each section was modeled according to a non-linear mixed model provided by J. Zell (email communication; modified from Zell et al. 2009), which is based on empirical estimates of decay from a broad range of tree taxa (T_k, T_R, Table 4.3). All sections in a log shared three attributes which influenced decay rate (T_k): tree-species-specific variation in decay (L_{decay}), log-specific variation
The ages of logs ($L_{\text{age}}$) present in the first year of the simulation were drawn from a folded normal distribution (a normal distribution for which only magnitude is considered – any negative numbers are “folded” into positive numbers) with a mean of 12 and a standard deviation of 17 years. This age distribution is realistic given reported half-life times of hardwoods (ranging from 2.3 to 30 years, Harmon et al. 1986) and results in a decay distribution similar to the one found in empirical surveys where decay stages are normally distributed with a peak at moderate decay stages (Chapter 3). New logs entering the landscape later in the simulation were assigned an age of 0. However, because the diameter of each section within a log ($T_{\text{diam}}$, Table 4.3) also influenced decay, sections within a log had slightly different decay rates. Although logs were not classified to specific species, I implied a variety of hardwood species by selecting a number ($L_{\text{decay}}$) from a normal distribution (Table 4.3). Large variation in decay rates among individual logs (Zell et al. 2009) was accounted for by assigning an additional

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Function</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$T_k$</td>
<td>Section decay rate</td>
<td>$e^{\beta_0 + \beta_1 T_{\text{diam}} + \beta_2 L_{\text{age}} + \beta_3 L_{\text{decay}} + \beta_4}$, where $\beta_0 = -3.96$, $\beta_1 = -1.20E-2$, $\beta_2 = 4.64E-2$, $\beta_3 = 5.04E-4$, $\beta_4 = -2.21E-7$</td>
<td>unitless</td>
</tr>
<tr>
<td>$T_R$</td>
<td>Percent of original density of section remaining</td>
<td>$100 - 100(1 - e^{-T_k (L_{\text{age}} - \text{lag})}) + L_{\text{decay}}$, where $\text{lag} = 1.2287$</td>
<td>%</td>
</tr>
<tr>
<td>$L_{\text{decay}}$</td>
<td>Species-specific variation from the standard decay rate</td>
<td>$\sim N(0,0.3129)$</td>
<td>unitless</td>
</tr>
<tr>
<td>$L_{\text{decay}}$</td>
<td>Log-specific variation from standard decay rate</td>
<td>$\sim N(0,10.1539)$</td>
<td>unitless</td>
</tr>
<tr>
<td>$L_{\text{age}}$</td>
<td>Log age</td>
<td>First year: $L_{\text{age}} \sim \text{folded} - N(12,17)$</td>
<td>years</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Subsequent years: 0</td>
<td></td>
</tr>
</tbody>
</table>

Source: 1) Decay rate is based on a model provided via email communication on March 31, 2010. Modified from Zell et al. (2009).
error term ($L_{\text{decay}}$) to each log (Table 4.3) which remained constant until the log decayed completely. The only climatological inputs required for the Zell et al. (2009) model of decay were average July temperature and the average annual precipitation, which data were acquired from the Louisiana Office of State Climatology ($t_j = 27.28$ °C, $p_y = 1600.2$ mm, [www.losc.lsu.edu](http://www.losc.lsu.edu), accessed March 30, 2010). Using these climatic data, the percent of the original density remaining in a section was calculated at the end of each model year (July 31).

This model of decay produces decay rates consistent with published decay schedules for coarse woody debris in Louisiana (Rice et al. 1997) in which 45-70% of the original mass in pumpkin ash logs remained after 30 months (7.5-20 cm diameter). The decay state (percent density remaining) of each log-section was updated yearly (Figure 4.1).

Sections were considered suitable for occupancy by passalid beetles when the percent original wood density remaining ($T_R$) was between 15.3% and 71.2%. These density values are associated with the traditional decay classifications 3 and 4 (Woodall and Williams 2005) which are strongly associated with passalid beetle occupancy (Chapter 3).

After sections decayed beyond 11% of their original density (well into decay class 5, assessed at the end of each year), those sections were removed and new logs were added until the total number of sections was equal to or just greater than a predetermined value (750 per ha = the estimated number of sections per ha in an empirical survey, Port Hudson census, Chapter 3), thereby maintaining a number of log-sections in the landscape near the pre-defined limit. This environmental stability was modeled in order to avoid the large expected effect that fluctuations in habitat availability would have on population dynamics and persistence (Lande 1993). The model could easily be modified to allow variation in yearly habitat availability if that were of interest.
Table 4.4 Parameterization of dispersal and reproduction submodels

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Function</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Transient phase (settle, search, step)</strong></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$D_{\text{dir}}$</td>
<td>Direction of movement in a four minute time step</td>
<td></td>
<td>radians</td>
</tr>
<tr>
<td></td>
<td>Step 1: $\sim U(-2\pi,2\pi)$</td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Step $&gt;1$: $\arctan2\left(\frac{\sin(\theta_{\text{CRW}}) + w_h\sin(\theta_h)}{1 + w_h}, \frac{\cos(\theta_{\text{CRW}}) + w_h\cos(\theta_h)}{1 + w_h}\right)$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\theta_{\text{CRW}}$</td>
<td>Contribution of a correlated random walk to movement direction$^1$</td>
<td>$D_{\text{dir},i-1} + 2\arctan\left(\frac{1 - \rho}{1 + \rho}\right)$, where $\rho = 0.96$</td>
<td>radians</td>
</tr>
<tr>
<td>$w_h$</td>
<td>Weight of search cues</td>
<td>$e^{B_M + B_P}$, where $B_M$ is the maternally inherited search cue sensitivity and $B_P$ is the paternally inherited search cue sensitivity</td>
<td></td>
</tr>
<tr>
<td>$\theta_h$</td>
<td>Mean distance-weighted direction of search cues within perceptual range</td>
<td>$\arctan2\left(\frac{\sum_{j=1}^{n} w_j\sin(\theta_j)}{\sum_{j=1}^{n} w_j\cos(\theta_j)}\right)$, where $w_j$ is the distance weighted strength of search cues, and $\theta_j$ is the direction to the center of cell $j$, $n$ is the number of cells with some portion within the perceptual range</td>
<td>radians</td>
</tr>
<tr>
<td>$w_j$</td>
<td>Distance weighted strength of search cues to center of cell $j$</td>
<td>$\frac{1}{pr}e^{-\frac{d_j}{pr}}$, $pr =$ perceptual range (m), $d =$ distance (m) to center of cell $j$.</td>
<td>unitless</td>
</tr>
<tr>
<td>$h$</td>
<td>Search cues considered in simulation experiment 1</td>
<td>$e^{\beta_0 + \epsilon}$, where $\beta_0 = -0.4149$, and $\epsilon \sim N(0, 0.9260)$</td>
<td>number</td>
</tr>
<tr>
<td>$D_{\text{dist}}$</td>
<td>Distance moved in a 2 min. interval</td>
<td></td>
<td>m</td>
</tr>
</tbody>
</table>

**Reproduction**

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Description</th>
<th>Function</th>
<th>Units</th>
</tr>
</thead>
<tbody>
<tr>
<td>$B_{\text{egg}}$</td>
<td>Characteristic of females; daily probability she will produce an egg</td>
<td>$\sim \text{Bern}(p)$, when $p = \frac{1}{1 + e^{-\beta_{\text{egg}}}}$, where $\beta_{\text{egg}} \sim N(\mu_{\text{egg}}, \sigma_{\text{egg}})$, $\mu_{\text{egg}} = -1.05, \sigma_{\text{egg}} = 0.8$ (see “Calibration”)</td>
<td>unitless</td>
</tr>
</tbody>
</table>

Sources: 1) (Zollner and Lima 1999, Fletcher 2006)
Dispersal

Dispersal began with a dispersal decision and then followed a loop through three processes: temporary settlement, search, and step (Figure 4.1, see “Transient Phase” below). This process (temporary settlement, search, step) repeated itself 30 times per day for 4 to 14 days (depending on the dispersal limitation treatment) until temporary settlement or death (see “Mortality”). Like forest edges are for *O. disjunctus* (Chapter 1), landscape edges were reflecting for model beetles. Four to fourteen days represent estimates of the length of time *O. disjunctus* would take to starve based on laboratory starvation experiments (Gross 2010). Although in my model settlement probability was fixed over time, an interesting addition to further investigations might allow choosiness to decline over time (e.g., Stamps et al. 2005). After temporary settlement, the probabilities that the beetle would mate (leading to permanent settlement) or disperse again were assessed.

Dispersal Decision

A decision to disperse was only considered by temporarily-settled adults (i.e. adults without a mate). Temporarily-settled adults had a daily probability of dispersing from a section \( P = 0.22 \), but this probability was set to 1.0 if a) another beetle pair occupied the section (this could occur when more than two beetles were temporarily-settled in the same log-section), or b) the section decayed beyond suitability (occurs only at the end of the year). The default dispersal rate \( P = 0.22 \) was based on the rate at which *O. disjunctus* left empty experimental logs (each 27.7 dm\(^2\)) over the course of a week in field experiments (Chapter 3).

Transient Phase

The transient phase (phase in between dispersal decision and temporary settlement) consisted of three parts: decision to settle, searching, and stepping.
**Decision to Settle**

The decision to settle led to temporary settlement which resulted in a reduced daily mortality rate and prevented a beetle from starving, but could only occur in log-sections of suitable decay that were unoccupied by a mated pair. In random order, each section within the beetle’s current grid-cell was considered for settlement \( P = 0.7973 \), the proportion of individual beetles that visited an empty 27.7 dm\(^2\) log when placed beside it in a habitat selection experiment, Chapter 3. All log-sections within a cell were given equal weight based on my assumption that a beetle could perceive each log-section within that distance more or less equally well (see perceptual range experiments in Chapter 3). If all sections were rejected or if all sections in a cell were occupied, then sections within the cell were not considered for settlement and were not included in the weights associated with orientation during search (next section) for the rest of the day. Preliminary analyses suggested that the ability to ignore a log-section after rejecting it was an important rule that prevented model beetles from continually returning to the same cell.

**Search**

The direction of the next move \( (D_{\text{dir}}, \text{Table 4.4}) \) was determined during the search phase. The first direction after dispersal was initiated was selected from a uniform circular distribution (Table 4.4). In the absence of search cues, beetles moved according to the rules of a correlated random walk which is defined by correlation in successive move directions (Turchin 1998). In empirically observed movements, naturally dispersing *O. disjunctus* exhibited an average correlation in subsequent moves of 0.96 (Jackson et al. 2009), which results in nearly straight movements and is close to the optimal linearity found in other simulation experiments (>0.9,
Search cues (habitat, mate, or conspecific density) were summarized by cell (h, Table 4.4). The average directions of search cues ($\theta_h$, Table 4.4) were averaged with the direction selected randomly according to the rules of a correlated random walk ($\theta_{CRW}$, Table 4.4) to determine movement direction (D$_{dir}$, Table 4.4). A beetle’s attraction toward cells was based on a) the number of suitable territories (habitat search), b) the number of territories occupied by potential mates (mate search), or c) the number of territories occupied by conspecific pairs (conspecific search) (Table 4.1). In this model, populations were sensitive to only one of the above cues, although the model could easily be extended to allow individuals to consider multiple variables at once. The value of each of the surrounding cells within a beetle’s perceptual range was weighted by the distance of its center to the center of the cell in which the beetle was located ($w_j$, Table 4.4).

As previously described in “State variables”, the strength of response to search cues varied along a continuum in Experiment One and were fixed (cue-responsive or cue-unresponsive) in Experiment Two. In Experiment One, a single gene controlled responsiveness to search cues. Cue responsiveness was modeled as a quantitative trait based on large allele variation at a single locus. For the sake of simplicity, I made the effects of each allele purely additive (i.e., no dominance) and allowed phenotype to be completely genetically determined (i.e., no environmental influence). In the initial population, the allelic effects (=contribution to the genotype) of each of an individual’s alleles (each individual inherited two) were drawn from a normal distribution with mean of 0 and standard deviation of 1. A similar model is available in quantiNEMO, a population genetic simulation tool (Neuenschwander et al. 2008). Although
quantitative traits that are completely determined by large variation at a single locus may not be common, large variation at a single locus does occur in nature and can produce significant phenotypic effects (Lee et al. 2010, Lutz et al. 2010). The genotypic value of this gene (=added value of both alleles) determined the strength of bias toward an attractant (habitat, mate, or conspecific density). A very low genotypic value resulted in a correlated random walk and a highly positive genotypic value resulted in hard turn toward the attractant. The genotypic value did not influence the distance from which a beetle could sense an attractant, but only the weight that an attractant within a predetermined perceptual range was given when determining the next move direction. In Experiment Two, this cue-responsiveness gene was again used, but all beetles were given the same genotypic value (2). Another gene was added, this one was a single-locus, maternally inherited regulatory gene that could turn “off” responsiveness to search cues. Half of the beetles in the original population carried the allele that turned off responsiveness to search cues. The goal in Experiment Two was to create two categorical phenotypes (strongly cue-responsive and cue-unresponsive) to allow simple comparisons of performance between individuals in the same population (comparisons of performance among individuals in different populations is complicated by variation in population density).

Only attractants in those cells within the perceptual range of a beetle were able to bias its movement. Perceptual range (the distance from which an individual could perceive a cue) was set to one cell (which includes all eight of the cells neighboring the beetle’s location), a distance based on an empirical test of *O. disjunctus*’ perceptual range (~1 m, Chapter 3).

**Step**

The distance encompassed by each step ($D_{\text{dist}}$) was drawn from a log-normal distribution (a common distribution for step-lengths, e.g., Schtickzelle and Baguette 2003, Haynes and
Cronin 2006, Jopp 2006) with parameters based on observed movement distances of naturally dispersing *O. disjunctus* (Table 4.4, see Jackson et al. 2009). A two minute time step was chosen because it resulted in movement distances between 0.5 and 1.5 m, approximately equal to a beetle’s perceptual range.

**Permanent Settlement and Mate Selection**

On the day after temporary settlement and on subsequent days thereafter, the probability of mating with an unmated beetle of the opposite sex was evaluated. Potential mates in the same log-section were given equal weight in a cumulative probability distribution from which a random number was drawn to determining the mate choice of a beetle. Probabilities of all potential mates summed to one. If mated, both beetles were considered “permanently-settled” and were subsequently unavailable to other potential mates. The section was then unavailable for temporary settlement and any other beetles in the section dispersed in the next time step. This mimics the pattern observed in settlement experiments (Chapter 3), in which rarely more than one mated pair remained in experimental logs after one week. If a beetle did not mate, it had a chance to disperse the next day (P = 0.22).

**Reproduction**

Females with a live mate had a constant daily probability (*B*$_{egg}$, Table 4.4) of laying an egg over a 40 day time period between May 1 and June 10. Continuous egg production during the breeding season has been well-documented (Gray 1946, Schuster and Schuster 1985). In order to replicate the large variability in fecundity in empirical data (Chapter 3), the probability of producing an egg each day was altered by a random variable assigned at birth to each female. Beetle-specific variation in fecundity as opposed to a simpler probability distribution was used in
order to replicate the wide variation in fecundity observed in experiments (Chapter 3). Birth parameters were also estimated by calibration with empirical data (see “Calibration”).

The juvenile stage lasted 110 days, after which a beetle was classified as an unmated, temporarily-settled adult (Figure 4.1). This length of time was used because although *O. disjunctus* ecloses into the adult stage after 80 days, young adults are not usually found outside the log (Jackson et al. 2009) and remain in the log for many weeks while their exoskeletons harden (Schuster and Schuster 1985).

**Mortality**

The model included three sources of juvenile mortality: 1) daily juvenile mortality (P = 0.009 based on mortality of juveniles observed in a field experiment, Chapter 3); 2) 100% juvenile mortality at the end of the year if a log-section became unsuitable; and 3) 100% juvenile mortality if both parents died, although the death of one parent did not affect the survival of offspring because similar sub-social insects such as wood-roaches and burying beetles provide care for offspring even when one mate is removed (Fetherston et al. 1994, Park and Choe 2002).

Adults had four sources of mortality: 1) daily mortality when in a log (P = 0.0025, based on adult mortality in logs in a field experiment, Chapter 3); 2) daily mortality when dispersing (P = 0.025), which was 10 times greater than when in a log in order to account for the probable increase in predation, injury, and/or dehydration (Belichon et al. 1996); the effect of this value is tested in my sensitivity analysis; 3) 100% mortality due to starvation at the end of the fourth, seventh, or fourteenth day of dispersal, depending on the dispersal limitation treatment; and 4) 100% mortality at the end of the third year of life.

This program was written in Fortran 90 and a one year run took 45 seconds.
Design of Simulation

Calibration

I calibrated important parameters for three processes for which direct data were not available: the parameters required for the midpoint displacement algorithm (\(H\) and \(\sigma\)), the input rate of log diameter classes, and the daily probability that a female produced an egg (Table 4.5). Calibration is the process of adjusting the value of an unknown parameter until the modeled process results in a pattern which matches a known standard. I calibrated my model to patterns observed during experiments and surveys. These observed patterns represent my best estimate of true behavior in the system, but are admittedly limited by the lack of temporal replication for empirical data.

Table 4.5 Parameters estimated via corroboration with empirical data.

<table>
<thead>
<tr>
<th>Pattern</th>
<th>Parameter</th>
<th>Description</th>
<th>Calibrated Values</th>
</tr>
</thead>
<tbody>
<tr>
<td>Spatial pattern of logs(^1)</td>
<td>(H)</td>
<td>related to fractal dimension (low = overdispersed, 1 = clustered)</td>
<td>0.0</td>
</tr>
<tr>
<td></td>
<td>(\sigma)</td>
<td>standard deviation</td>
<td>1.0</td>
</tr>
<tr>
<td>Yearly rate of log-diameter input (cm)(^1) (cumulative distribution)</td>
<td>(L_{\text{diam}})</td>
<td>Diameter class (Cumulative Distribution): 7-10 (0.50022), 10-15 (0.77922), 15-20 (0.90939), 20-25 (0.96409), 25-30 (0.98598), 30-35 (0.99456), 35-40 (0.99790), 40-45 (0.99919), 45-50 (0.99969), 50-55 (0.99992), 55-60 (1.00000)</td>
<td></td>
</tr>
<tr>
<td>Daily egg production(^2)</td>
<td>(\mu_{\text{egg}})</td>
<td>Mean in the daily log-odds of egg production ((\beta_{\text{egg}})) of individual female beetles</td>
<td>-1.05</td>
</tr>
<tr>
<td></td>
<td>(\sigma_{\text{egg}})</td>
<td>Standard deviation in (\beta_{\text{egg}})</td>
<td>0.8</td>
</tr>
</tbody>
</table>

Source: 1. Port Hudson Census (Chapter 3); 2. Field experiments conducted near Baton Rouge, LA (Chapter 3)

Spatial Pattern of Logs \((H, \sigma)\)

The spatial distribution of logs was determined by a fractal distribution of log-odds that a log would be centered in a cell. The calibrated parameters were \(H\) (related to fractal dimension;
H = 0 leads to a random distribution and H = 1 leads to aggregation) and \( \sigma \) (standard deviation of normal distribution from which random values were drawn). I ran just the landscape portion of the simulation model (50 years with no beetles) using a full factorial combination of H (0.0, 0.5, 1.0) and \( \sigma \) (0.5, 1.0, 1.5), with three replicates for each treatment combination. I compared the simulated distribution of logs with an empirical distribution from data collected in a 250 X 250 mixed forest landscape (Port Hudson Census, Chapter 3). Ripley’s L-function (Venables and Ripley 2002), a variance stabilized estimate of aggregation, was calculated for each landscape (including the real landscape) for distances every 5 meters from 5 to 50 m. I compared Ripley’s L-function by calculating the sum of the squared differences between the empirical and simulated estimates at each distance. The landscape with the lowest mean-squared differences with the real landscape was selected. Although my empirical data are limited to one landscape at one point in time, the calibration of my model with an empirical distribution of coarse woody debris incorporates a degree of small scale (meters) realism that is not common to forest models, which often place woody pieces or live trees randomly (Jonsson et al. 2003, Takenaka 2005) or according to an undescribed algorithm (Perez and Dragicevic 2010).

**Diameter (L\( _{\text{diam}} \)) Distribution of Logs**

I developed a distribution of yearly input rates for logs of different diameter classes. For diameter distribution to remain constant over time (and for the sake of reducing a potentially important source of stochasticity), small diameter logs were input at a greater rate than large diameter logs, because large-diameter logs decayed more slowly. I manually altered the input rates for each diameter class and ran the model for 150 years. I compared histograms of the empirical and simulated distributions by eye.
Reproduction ($\mu_{\text{egg}}, \sigma_{\text{egg}}$)

The characteristic daily probability that a female would lay an egg was determined by calibrating the distribution of larvae per nest after 80 days with an empirically-based distribution of larval number. The empirical data were from an experiment in which larvae were censused after parents had been released in 27.7 dm$^2$ logs for 80 days (large, one-couple logs in Chapter 3 performance experiments). I used the reproduction submodel in which egg production and juvenile mortality were simulated over a period of 80 days. I manipulated two parameters, $\mu_{\text{egg}}$ and $\sigma_{\text{egg}}$, which described a normal distribution of $\beta_{\text{egg}}$, the daily log-odds that a female would produce an egg during the reproductive season ($\beta_{\text{egg}}$ was fixed for each female at the beginning of the simulation). A broad range of $\mu_{\text{egg}}$ and $\sigma_{\text{egg}}$ values were tested with 1000 females per test. These fecundity parameters ($\mu_{\text{egg}}$ and $\sigma_{\text{egg}}$) were continually adjusted until the final distribution of larval numbers was not statistically different from empirical observations, as determined by a t-test (to compare means) and a Kolmogorov-Smirnov test (to compare distributions).

Simulation Experiments

Summary

I conducted two simulation experiments testing the effects of search strategy and dispersal limitation on population distribution and individual fitness. In Experiment One, I tested how cue responsiveness in a population affects the density-area relationship and incidence after 100 years of cue evolution. By allowing cue-responsiveness alleles to be heritable, I was able to evaluate changes in naturally-selected genotypic values for cue-responsiveness over time. In Experiment Two, I evaluated the fitness consequences of cue-responsiveness by allowing unresponsive individuals into the population with whom to compare with cue-responsive individuals.
Experiment One

For Experiment One, I tested the effect of three search strategies (habitat, mate, and conspecific search) on distribution and genotypic value. For all three strategies, the strength of attraction was based on the number of attractants per cell and the genotypic value of their cue-responsiveness alleles. I also varied the time to starvation during dispersal in order to test the effects of dispersal limitation on the importance of search strategies. Six replicate simulations were run for each treatment combination.

Emergent Population and Landscape Level Patterns

I analyzed the effect of cue use on density-area, immigration-area, emigration-area, incidence-area relationships, and genotypic value.

Density-area, immigration-area, and emigration-area relationships were calculated using separate simple linear regression models for which the responses were 1) density = number of individuals in a log divided by the number of territories in a log (see Hambäck and Englund 2005), 2) immigration per area = number of immigrants in a log divided by the number of territories in a log (note this is per area not the more common value per capita, see Englund and Hambäck 2007), and 3) emigration per capita = number of emigrants from a log divided by the number of adults (including parents and newly matured juveniles) present in the log at the beginning of the dispersal season (see Englund and Hambäck 2004). Note that density, immigration, and emigration are all summarized at the log level such that settlement within and among territories within the same patch was not differentiated. This model does not differentiate beetles who stay in their natal territory and those who move to a different territory within the same log. Each ln-transformed response was predicted by the ln-transformed number of territories in a log. Following the procedure of Englund and Hambäck (Hambäck and Englund
2005, Englund and Hamback 2007), density and immigration per area values were averaged across logs of the same size to avoid the presence of zeroes in the analysis. The parameters of interest from these regression models were both a) the slope of density (immigration or emigration) over area (called the density-area effect) and b) the intercept of the equation, which indicates the baseline density, immigration, or emigration. These values are not expected to be independent. I averaged the a) slope and b) intercept across replicates to estimate the average area relationship.

The incidence-area relationship was also evaluated in order to allow for direct comparisons with the average incidence-area relationship observed over 22 forest plots in Louisiana (Chapter 3). I used a mixed-effect logistic regression in which the presence of a beetle couple in a territory was the response and the size of the patch (ln-transformed number of territories in a log) and an indicator of territory suitability (i.e., adequate decay) were predictors. Log ID was a random effect to account for non-independence within logs.

The average estimate for each response was calculated using a linear regression in which search strategy, dispersal limitation, and their interaction were predictors (R Development Core Team 2010).

**Experiment Two**

Experiment Two was designed to more thoroughly investigate the fitness benefits of cues evolved in Experiment One. Two categorical genotypes were present in each population: cue-responsive and cue-unresponsive. The purpose of this experiment was to allow explicit comparisons of cue-responsive vs. random search within the same population. Comparisons between different populations suffered from the confounding effects of changes in population size, which in turn influenced the fitness value of a cue. The genotypic value for all cue-
responsive individuals was fixed at 2 (meaning the direction of a cue received $e^2 = 7.4X$ the weight of the linear direction). A second haploid, maternally inherited allele was introduced which determined whether or not an individual’s cue-responsiveness was “turned on”. Individuals carrying the cue-unresponsive allele became random searchers. The second simulation started with 50% of the population carrying the cue-unresponsive allele and was run for five years – just long enough to allow differences in fitness between cue-responsive and cue-unresponsive individuals to be apparent but short enough to prevent fixation or extremely small numbers of one phenotype.

**Relative Performance Associated with Search Strategy**

I compared the performance of cue-responsive individuals to cue-unresponsive individuals using six relative measures. The geometric mean relative fitness of cue-responsive genotypes to cue-unresponsive genotypes was calculated according to the equation:

$$r = \frac{1}{4} \ln \left( \frac{P_2 \times q_1}{q_7 \times P_1} \right)$$

(4.1)

where $p$ and $q$ refer to the frequency of cue-responsive and cue-unresponsive genotypes, respectively, among adults in the seventh and first years (Gillespie 1973, Friedenberg 2003). As a measure of the relative change in genotype frequency in the population over time, the geometric mean relative fitness is a direct measure of a genotype’s fitness (=contribution to genotypes in subsequent generations) (Gillespie 1973, Friedenberg 2003). Six replicates of each treatment were performed to separate the effects of selection from the effects of genetic drift.

The remaining five relative measures were dispersal mortality (number of deaths during dispersal per number of adults attempting dispersal), mate success (number mated and/or with live offspring on last day/total number of adults), number of dispersal events per beetle (successfully mated beetles only), average dispersal time per trip (number of steps per number of
successful trips), and average net displacement (straight line distance between natal and settlement habitat, successful dispersers only). As an indicator of mobility, net displacement can indicate the spatial scale of interactions among individuals (Kindvall et al. 1998) and can be used to predict population spread (Haydon et al. 2008). Because the numbers of young were similar for all successful mating pairs, fecundity of successfully mated pairs was not included in my analysis of performance. Overall mortality closely mirrored dispersal mortality, and only dispersal mortality estimates are reported. Performance measures were measured for first year adults at the end of the seventh year of the simulation.

The relative performance measures (excluding relative fitness) were calculate as (cue-responsive – cue-unresponsive)/(cue-responsive + cue-unresponsive) which resulted in values ranging between -1 (relatively low) and 1 (relatively high) (Conradt et al. 2003, Fletcher 2006). All performance responses were measured together in a single multivariate linear regression for which search strategy was the independent variable.

Sensitivity Analyses

The model was tested for sensitivity to four demographic parameters: birth rate (the daily probability that an individual female will lay an egg), adult mortality (the daily probability that a temporarily-settled or permanently-settled adult will die), starting incidence (year 0), and dispersal mortality (the daily probability that a dispersing adult will die). Birth rate and adult mortality rates were tested at values ±20% the default value which equated to 0.21 and 0.31 probability of laying an egg per day during the reproductive season (birth rate) and 0.002 and 0.003 probability of death within a log per day (adult mortality). The default starting incidence was 0.22, which I varied from one half (0.11) to two times (0.44) that amount. By default, dispersal mortality was 10X the default adult mortality (0.025 per day) and I tested dispersal
mortality equal to adult mortality (0.0025 per day) and 100X adult mortality (0.25 per day). For each demographic parameter, the effects of these changes on incidence and genotypic values after 100 years were evaluated in two linear regression models in which incidence (first model) and genotypic values (second model) were the response variables and the demographic parameter was the independent variable.

RESULTS

Calibration

Spatial Distribution of Logs

Landscapes with low global aggregation (H=0.0) and moderate standard deviation (σ = 1.0) exhibited the smallest differences in aggregation with the empirical landscape (measured by comparing Ripley’s L-function). Low H was associated with low spatial autocorrelation at the global scale (the scale of the entire map), and moderate σ resulted in locally spatially auto-

Figure 4.2 Empirical and simulated landscapes. Each dot represents a single log-section and each linear array of dots indicates a log.
correlated logs with gaps between clusters (Figure 4.2). Global autocorrelation (high H), on the other hand, led to the unrealistic situation in which large sections of the landscape were without logs.

**Diameter (L_diam) Distribution of Logs**

Calibrated log diameter distribution remained reasonably constant over time and was similar to the observed distribution from my single-point in time survey of coarse woody debris in a forest (Figure 4.3). The most realistic input rates strongly favored small logs. Logs under 10 cm in diameter comprised 54.5% of the new logs each year. Only three of every 10,000 logs were in the greatest size class (0.55-0.60 m).

![Diameter (L_diam) Distribution of Logs](image)

**Figure 4.3. Calibrated and observed distribution of log diameter.**

**Reproduction and Juvenile Mortality**

The empirical distribution of offspring number was well-replicated by fitting the daily probability that a mated female would produce an egg to a normal distribution of log-odds values.
with mean of -1.05 and a standard deviation of 0.8 (t_{df=6} = 0.823, P = 0.44, Kolmogorov-Smirnov D = 0.28, P = 0.64). A distribution of offspring number with a mean of 6.81 (range = 0-20) was produced.

Simulation Experiments

Experiment One

Emergent Population and Landscape Level Patterns

Density increased with area for all treatments, and the strength of the density-area relationship generally increased as dispersal limitation increased (Figure 4.4a). Conspecific search and random search yielded the strongest density-area relationships when dispersal limitation was low (14 days) and medium (7 days), but resulted in extinction when dispersal limitation was high (4 days, Figure 4.4a). Mate and habitat search resulted in similar density-area relationships when dispersal was low, but the slope between density and area was greater for habitat search when dispersal limitation was medium, and greater for mate search when dispersal limitation was high (Figure 4.4a). Habitat search consistently resulted in greater abundances in small logs than other search strategies (Figure 4.4b), although mate search resulted in abundances nearly as high when dispersal limitation was low or moderate. The lowest abundances per patch were observed in random search populations (Figure 4.4b).

Immigration into a patch (=log) decreased with increasing patch-area in all treatments (Figure 4.4c), but declined most rapidly for populations using habitat search (slope = -0.24 to -0.40). When dispersal limitation was moderate, random and conspecific search resulted in greater density-area effects than mate or habitat search (Figure 4.4a), a difference which was associated with a large drop in the number of immigrants into small patches in these populations
Figure 4.4 Density-area (a), immigration-area (c), and emigration-area (e) effects associated with search strategy (random, habitat, mate, conspecific search) and dispersal limitation (low=14 days, medium=7 days, and high=4 days). Area-corrected values indicate the density (b), number of immigrants (d), and number of emigrants (f), expected from a patch with only one territory.

(Figure 4.4d), but not a change in immigration scaling (Figure 4.4c). Likewise, the strong density-area relationship in mate search populations when dispersal limitation was high (Figure 4.4a) was associated with a drop in the numbers of immigrants into small patches (Figure 4.4d).
Figure 4.5 Incidence is associated with dispersal limitation (low=14 days, medium=7 days, and high=4 days) and search strategy (random, habitat, mate, conspecific search).

Figure 4.6 Incidence-area relationship observed when model beetles used one of four different search strategies (random, habitat, mate, conspecific). The incidence-area relationship observed in 22 forest plots (Chapter 3) is also presented (solid line). Dispersal limitation (time to starvation during dispersal) was a) low (14 days), b) medium (7 days), and c) high (4 days). Random and conspecific search are not depicted with high dispersal limitation because those populations went extinct.
Emigration decreased with patch-size for all search strategies, but the emigration-area effect was particularly strong when habitat search was used (Figure 4.4e). Furthermore, the baseline emigration rate from the smallest patches was lower for habitat search (Figure 4.4f). Baseline emigration was highest in conspecific and random search populations (Figure 4.4f). Emigration scaling with area tended to increase with dispersal limitation (Figure 4.4e).

Habitat and mate search resulted in high incidence regardless of dispersal limitation, but random and conspecific strategies resulted in greater variation with dispersal limitation such that extinction occurred when dispersal limitation was high (4 days, Figure 4.5). All strategies (including random search) resulted in high incidence ($\approx 0.5$) when dispersal limitation was low, with mate search resulting in the highest overall incidence (0.54) which was 3%, 5%, and 13% greater than habitat, conspecific, and random search, respectively. Habitat search resulted in 1% and 14% greater incidence than mate search in medium and high dispersal limitation treatments, respectively.

![Figure 4.7 Change in average genotypic values over 100 years of cue evolution when dispersal limitation is low (14 days, a), medium (7 days, b), and high (4 days, b). Genotypic value for each individual is the added effect of its cue-linked alleles.](image)

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Although the incidence-area relationship was positive for all treatments, the incidence-area relationship was greatest when conspecific search was used (0.29-0.35, Figure 4.6), resulting in a slope most similar to (although still quite different from) the empirically derived slope (=0.45). Mate search resulted in the lowest incidence-area relationships (0.12-0.12) with random and habitat search producing moderate slopes (habitat > random). As dispersal limitation increased, the incidence-area relationship increased.

Bias toward cues (=average genotypic values, or added effect of alleles associated with a trait) increased during the first few years as population size increased for all search strategies in all dispersal limitation treatments (Figure 4.7), but conspecific search genotypic values started to decline after 20 years (earlier when dispersal limitation was low) and habitat search genotypic values started to decline after 25 years (Figure 4.7). Mate search genotypic values continued to rise throughout all treatments, though the rate of increase declined over time as values reached the limits of original allele variation. Although the average genotypic value for each search strategy was quite different (mate > habitat > conspecific), none of the search strategies were selected against. Mate search ended with the largest genotypic value (~1.84 in all dispersal limitation treatments, respectively), a value associated with a six fold bias toward mates ($e^{1.84}=6$, bias is measured relative to the correlated random walk). The final effect size for conspecific search (-0.47 - -0.31) resulted in only a weak bias toward conspecifics ($e^{-0.47}=62%$ the weight of a correlated random walk).

**Experiment Two**

**Relative Performance Associated with Search Strategy**

Relative fitness was greatest for mate searchers when dispersal mortality was low, but greatest for habitat searchers when dispersal mortality was moderate or high (Figure 4.8). In the
low dispersal limitation treatments, mate search led to greater relative dispersal mortality than habitat search but greater mating success. Mate search also led to a consistent pattern of reduced numbers of dispersal events presumably because permanent settlement (i.e., mating) quickly followed temporary settlement. Habitat search resulted in generally reduced relative dispersal mortality, high relative mating success (except for when dispersal was least limited), relatively fewer steps per trip, and lower relative net displacement than other strategies (Figure 4.8). Conspecific search owed its lower relative fitness, lower relative mating success, and greater relative dispersal mortality in part to having little decrease in the numbers of steps per dispersal.
event (leading to greater risk of starvation). Both habitat and conspecific search increased in relative fitness as dispersal limitation increased.

Sensitivity Analyses

Sensitivity of incidence to demographic parameters depended on search strategy (Figure 4.9). Overall, conspecific search and especially random search were associated with strong sensitivity of incidence to changes in demographic parameters. A reduction in birth rate of 20%, an increase in adult mortality of 20%, and a 10-fold increase in dispersal mortality resulted in

Figure 4.9 Sensitivity of I) incidence and II) average genotypic value to a) birth rate (0.21, 0.26, 0.31 per day), b) mortality (0.0020, 0.0025, 0.0030 per day), c) starting incidence (0.11, 0.22, 0.44), and d) dispersal mortality (0.0025, 0.025, 0.25 per day). Missing bars indicate the extinction of populations in that treatment combination.
extinction of random and conspecific search populations. Random search populations also went
extinct when density started at 50% the default value, but conspecific search populations suffered
only a 22% reduction in incidence (Figure 4.9). Habitat search was associated with moderate
sensitivity of incidence to within-log parameters (±20% birth rate: -30% - +1%; ±20% adult
mortality: +15% - -93%), but low sensitivity to dispersal mortality (100-fold increase over
normal: -42% incidence, Figure 4.9). Mate search was associated with strong sensitivity of
incidence to strongly increased dispersal mortality (100-fold increase: -98% incidence, but
conferred low sensitivity to changes in birth rate (-8% - +2%) and moderate sensitivity to adult
mortality (+15% - -19%, Figure 4.9).

Genotypic values were much less sensitive than incidence to changes in demographic
parameters with a few exceptions (Figure 4.9). Habitat search genotypic values were generally
low (≈ 0.0 which means habitat bias was weighted equally with the correlated random walk
when determining orientation) but ended at higher values when adult and dispersal mortality
were high (+0.95 = 2.6X correlated random walk). Mate search genotypic values were
consistently high (≈1.74 = 5.7X correlated random walk), but decreased to 1.30 when dispersal
mortality was high. Conspecific search genotype values were consistently low (≈ -0.30 = 26%
lower weight than correlated random walk) regardless of demographic changes.

**DISCUSSION**

**Search Strategy and the Density-Area Relationship**

The density-area relationship was positive for all search strategies, but varied strongly
with search strategy and dispersal limitation. A novel outcome of this model was the finding that
mate search generally resulted in a weak density-area relationship suggesting that far from
mimicking the effects of conspecific search on distribution, mate search affects distribution in a
unique way. High immigration into small patches by mate searchers supports the hypothesis that
mate search promotes incidence in small patches by overcoming mate limitation (e.g., Fagan et
al. 2010). Although not investigated with explicit attention to its effect on density-area
relationships, mate search has long been recognized as an important behavior enabling the
persistence of smaller populations (Hopper and Roush 1993, McCarthy 1997). Here I show that
in a spatially fragmented system with a majority of small patches, mate search maintains large
overall incidence in large part by maintaining high immigration into small patches.

Habitat search was much less sensitive to dispersal limitation than other strategies,
resulting in consistently high incidence across dispersal limitation treatments. Not only did
habitat search maintain successful dispersal into small patches relative to other strategies when
dispersal was limited, but habitat search strongly inhibited emigration, especially from large
logs. When using the habitat search strategy, model beetles biased their movements away from
the matrix, effectively following the length of the log until available habitat was found or the end
of the log was reached. This replicates my observation that when naturally dispersing \textit{O.
disjunctus} encounters a log, it usually follows the log along its length (H.B.J., personal
observation). Many animals bias movement away from the matrix when confronted with a patch
edge (Haddad and Baum 1999, Ries and Debinski 2001, Conradt et al. 2003, Cronin 2003b,
Schtickzelle and Baguette 2003, Fried et al. 2005, Crone and Schultz 2008, Reeve et al. 2008a,
Jackson et al. 2009, Reeve and Cronin 2010). This pattern has important implications for
population persistence because a change in emigration rates that disproportionately decreases
emigration from large patches is expected to reduce the extinction risk of the entire
metapopulation (see Kindvall and Petersson 2000).
My model indicates that a strong positive density area relationship may be more indicative of a failure of immigration to supplement vulnerable populations on small patches (e.g., rescue effects, Brown and Kodric-Brown 1977) than of successful immigration into large patches. This is consistent with theory suggesting that movement behavior will have less effect on density within a patch as isolation or dispersal limitation increases, but that within-patch processes (e.g., greater risk of extinction associated with low population size in small patches, MacArthur and Wilson 1967, or edge effects, Paton 1994) will be more likely to dictate the pattern of density within patches (Hambäck and Englund 2005, Östman et al. 2009). My model provides the further insight that simple measures of dispersal limitation or isolation will not completely predict the relative impact of within- vs. among- patch processes on the density-area relationship, but that the search strategy employed by a species will strongly influence the success with which populations on small patches are rescued from extinction.

Virtual Migration (Hanski et al. 2000) is a popular model of movement that provides inferences about rates of mortality, emigration, and immigration from mark-recapture data, and allows estimates of immigration and emigration to vary with patch size. My data can improve insights from this model by suggesting mechanisms leading to the estimated area-scaling in immigration and emigration rates. For example, my data suggest that strong scaling of area with immigration and emigration is likely to indicate biased movement at habitat boundaries.

**Strength of Response to Cues**

My data lead to the hypotheses that the fitness benefits of mate cues do not change with dispersal limitation (the benefit is always high), but response to habitat and conspecific cues will be most beneficial when dispersal is time-limited by energy constraints. In a simulation experiment designed to compare habitat and mate search strategies, Jonsson et al. (2003) found
that mate search almost always outperformed habitat search in terms of efficiency (=time until a mate was found), and yet some of the fungivorous species on which their model was based responded almost exclusively to habitat cues (Jonsson et al. 1997). I suggest the possibility that low energy reserves during dispersal may explain heavy reliance on habitat search in some taxa, because energy-limited individuals benefit from frequent stops to forage (e.g., Zollner and Lima 2005). Supporting this hypothesis is the finding that one habitat-cue dependent species considered in the study of Jonsson et al. (2003), the ciid beetle *Cis quadridens*, is also one of the few distance-limited species in the system (Jonsson and Nordlander 2006). The desperate larvae hypothesis (Knight-Jones 1953) is a similar hypothesis to ours which considers variation in responsiveness to habitat cues within individuals rather than among populations, and predicts that individuals will become more responsive to habitat cues as their energy reserves are depleted and has found empirical support in patterns of habitat settlement among marine larvae (e.g., Botello and Krug 2006). Support for my hypothesis that variation among species in response to habitat cues is associated with species-specific starvation-related dispersal limitation will require more data concerning both energy-related time limits to dispersal (or correlates such as body size, Marshall and Keough 2003, Alexander 2005, Reim et al. 2006, Jenkins et al. 2007) and cue-use of species.

By design, the primary benefit of conspecific attraction in my model was reduced search time, as opposed to benefits identified for other systems such as when conspecifics provide information concerning habitat quality (Doligez et al. 2002, reviewed in Danchin et al. 2004, Doligez et al. 2004, reviewed in Dall et al. 2005, Nocera et al. 2006), help to prevent predation (Zuberbuhler et al. 1997, Nelson and Jackson 2008, Favreau et al. 2010), or improve resource acquisition (Anderson 1991, Jarvis et al. 1998, see Stamps 2001 for discussion of ultimate and
proximate causes of conspecific attraction). Although it has been considered theoretically (Stamps 2001, Fletcher 2006), few studies have documented the ability of conspecific attraction to reduce search time (but see Ruczynski et al. 2007, Ruczynski et al. 2009). Further empirical research should a) document the association between conspecific attraction and search time and b) investigate whether sensitivity to conspecific attraction during search increases as dispersal limitation increases, as predicted by my model.

The hypothesis that the strength of habitat attraction will depend on dispersal limitation is similar to the more landscape-oriented hypothesis that bias toward habitat will be strongest in fragmented habitat (Schtickzelle and Baguette 2003, Barton et al. 2009). My model further indicates, however, that the strength of habitat attraction will be reduced as local population density increases. The result in my model was a decline in responsiveness to habitat cues after an initial rise such that in the final generation model beetles made only a moderate turn toward habitat when it was in their perceptual range.

Search Strategies and *O. disjunctus* Distribution

Although none of the tested search strategies resulted in an incidence-area relationship as strong as that found in my empirical surveys, conspecific attraction was closest. I can think of two reasons why the model may not have replicated the strength of the empirical incidence-area relationship. First, *O. disjunctus* uses all three cues but I considered only one cue at a time. How multiple cues interact to influence distribution is unknown and represents a potentially fertile area for future research. Second, incidence in the model was higher than in empirical surveys. That high overall densities leave less room for variation to be observed among patches of different size makes intuitive sense and is consistent with another study of scaling in abundance across scales. Burrows et al. (2009) found that moderate proportional incidence (i.e., the
proportion of sites in which a species was present) was the best predictor of a steep slope between variation in abundance of intertidal species and spatial scale, and that only after taking incidence into account could important biological patterns associated with dispersal mode and trophic pattern be distinguished. Hence, when using patterns of variation in incidence among habitats to infer underlying mechanisms the overall incidence should be taken into account.

That modeled search strategies resulted in higher incidence rates than I found in forests, suggests that some key limitation on *O. disjunctus* population size was not included in the model. One potential limitation to *O. disjunctus* incidence is interspecific competition. In a survey of *O. disjunctus* distribution in 22 forest plots, I found that the odds of finding *O. disjunctus* in a log-section were reduced by 50% when ants (various species) were present (Chapter 3). Competitive interactions with ants have not been experimentally tested, but the fact that ants were found in 41% of log-sections suggests that ants have the potential to significantly limit *O. disjunctus* incidence. Parasitism and predation may also limit *O. disjunctus* incidence. Tachinid fly parasitoids have been reared from passalid larvae, but their rate of parasitism is unknown. Although a potential benefit of rearing young in coarse woody debris is protection from other forms of predation, at least one study noted that passalid beetles were the primary source of animal protein for black bear in west-central Florida (Brown 2004). The benefit of this model is that additional realism can be easily incorporated for future investigation of interspecific effects.

**Conclusion**

Studies in spatial ecology often focus on the interaction between the dispersal ability of a species and the configuration of its environment to predict the resilience of a population to anthropogenic habitat alteration (Louy et al. 2007, Hendrickx et al. 2009, Blanchet et al. 2010). My study emphasizes that a third factor can be just as important: the ability of a species to
respond to habitat, mates, or conspecifics. Continued supplementation of small patch populations with immigrants when habitat and mate search are used and decreased emigration when habitat search is used may be particularly important factors that can ameliorate the effects of increased isolation. Hence, there is potential for search strategies to explain what simple measures of mobility have not. Although many studies suggest that low mobility is a risk factor when habitat is scarce (Karr 1982, de Vries et al. 1996, Louy et al. 2007, Hendrickx et al. 2009), other studies have found that moderate (Blanchet et al. 2010) or high (Gibbs 1998, Van Houtan et al. 2007) mobility is associated with vulnerability to change. I suggest that cue use may help to resolve these inconsistencies.
Chapter 5: Discussion

SUMMARY

The objective of this dissertation was to contribute to our understanding of how processes acting at multiple spatial scales influence species incidence by integrating information from dispersal and habitat selection experiments with the multi-scaled pattern of incidence of *O. disjunctus* (Figure 5.1). The most striking pattern to emerge from these data is the strong influence of fine-scale behaviors and environmental filters on incidence.

The strongest patterns and processes associated with incidence operated at the level of individual territories (Figure 5.1), which my performance experiments indicated had a minimum surface area of 27 dm², and at which level decay was the most important environmental correlate. Incidence within territories on the same log was correlated, a pattern of aggregation that might be associated with conspecific attraction observed during immigration into a territory-sized log. Immigration associated with conspecific attraction was balanced by emigration, spacing which served to prevent the negative density-dependent growth I observed in territory-sized logs when other beetle pairs were forced to be present. Log-size was the strongest environmental correlate of incidence at local scales, a pattern that may be associated with the preference *O. disjunctus* showed for larger territories during habitat selection experiments. Dispersal among territories in my habitat selection experiment was limited within 5-10 m for most beetles, which may have led to the correlation in incidence among logs within the same region (subplot) in my field survey. The lack of strong dispersal among subplots within a forest may explain why incidence at that scale was relatively independent. Flood history was a strong correlate of incidence among forests, but forest cover explained less variation in incidence than expected, given the low mobility of *O. disjunctus*. A simulation model of movement,
reproduction, and mortality over 100 years suggests that the high incidence of *O. disjunctus* within forest plots could be explained by the dispersal efficiency conferred by the use of habitat cues at fine-scales.

**SYNTHESIS**

These studies demonstrate the potential for sophisticated multi-scale observations of incidence linked to mechanistic experiments by a biologically relevant simulation model, to make strong inferences regarding the environmental variables and mechanisms underlying distribution. Together, these findings provide two major insights: 1) environmental filters and behaviors at fine-scales (e.g., within the neighborhood of individuals) may be most important to species incidence; and 2) low-mobility at fine-scales does not equate to high susceptibility to forest loss, but rather the effect of habitat loss on incidence will probably depend on the information animals use during dispersal.

**The Importance of Fine-Scale Processes**

A central problem in ecology is that of predicting patterns of variation (=aggregation) in distribution across scale (Levin 1992). My data suggest the importance of environmental factors and behavioral traits that operate within the response range of an organism (i.e., the distance at which individuals exhibit a response to phenomena). A meta-analysis investigating the distribution of marine benthic organisms suggests that strong fine-scale variation may be a general pattern (Fraschetti et al. 2005). Fine-scale variation may be generally expected to overshadow variation at larger scales for two reasons: 1) dispersal limitation and 2) non-random individual behavior. Dispersal limitation can prevent individuals from settling in optimal habitat, therefore I might expect the signal of species-environment relationships to be greatest at fine-scales where “habitat matching” (Pinto and MacDougall 2010) is most likely to occur. For
mobile organisms, habitat matching is more pronounced when animals engage in non-random movement behavior, i.e., when animals direct their movement and settlement based on information in their environment (Clobert et al. 2009). If non-random movement leads to settlement in optimal habitat, then it can be expected to intensify the effects of any changes in fecundity and mortality associated with that habitat on incidence, thereby increasing the strength of variation at fine-scales, for example by increasing the density of individuals in large logs as I found in my simulation model.

Admittedly, this conclusion is limited by the scales at which I observed *O. disjunctus* incidence. Had I expanded the hierarchical survey to include the entire range of *O. disjunctus* then I would expect to see an increase in the importance of large-scale climatic variation as well as other factors which might limit a species toward the edge of its range.

When Low Mobility Leads to High Landscape-Level Incidence

Non-random movement behavior not only alters local variation in incidence, but as my model showed, can “scale up” to alter large-scale variation in incidence. Although low mobility is often associated with vulnerability to large-scale habitat disturbance (Karr 1982, de Vries et al. 1996, Louy et al. 2007, Hendrickx et al. 2009), the distribution of *O. disjunctus* illustrates that informed dispersal can ensure that a species with low mobility is no longer dispersal limited (see also Diekötter et al. 2010). On the other hand, inefficient or maladaptive (e.g., ecological trap, Battin 2004) search strategies could explain why some studies have found that moderate (Blanchet et al. 2010) or high (Gibbs 1998, Van Houtan et al. 2007) mobility is associated with vulnerability to change. Further research should investigate the potential for cue use to resolve inconsistencies in the relationship between mobility and large-scale incidence.
Figure 5.1 Conceptual model summarizing findings concerning the environmental correlates (plain font) and behaviors (italicized) associated with *O. disjunctus* incidence at four spatial extents (bold): microhabitat, local, regional, landscape.


Botello, G. and P. J. Krug. 2006. 'Desperate larvae' revisited: age, energy and experience affect sensitivity to settlement cues in larvae of the gastropod Alderia spp. Marine Ecology-Progress Series 312:149-159.


spatial autocorrelation in the analysis of species distributional data: a review. Ecography 30:609-628.


# Appendix 1 – Sampling Locations for Chapter 3

Table A1.1 Sampling locations for multi-scale regional survey.

<table>
<thead>
<tr>
<th>Forest</th>
<th>Plot</th>
<th>Easting</th>
<th>Northing</th>
<th>Date Sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Grand Cote NWR(^1)</td>
<td>1</td>
<td>582370</td>
<td>3441441</td>
<td>4-May-06</td>
</tr>
<tr>
<td>Sherburne WMA(^2)</td>
<td>2</td>
<td>621427</td>
<td>3378385</td>
<td>4-Apr-06</td>
</tr>
<tr>
<td>Cat Island NWR(^1)</td>
<td>3</td>
<td>646191</td>
<td>3403973</td>
<td>20-Apr-06</td>
</tr>
<tr>
<td>Sherburne WMA(^2)</td>
<td>4</td>
<td>628831</td>
<td>3363061</td>
<td>23-Mar-06</td>
</tr>
<tr>
<td>West Baton Rouge Parish(^3)</td>
<td>5</td>
<td>656120</td>
<td>3381734</td>
<td>9-Apr-06</td>
</tr>
<tr>
<td>Dewey M. Wills WMA(^2) (Lake Larto)</td>
<td>6</td>
<td>603922</td>
<td>3472214</td>
<td>24-May-06</td>
</tr>
<tr>
<td>St. Landry Parish(^3)</td>
<td>7</td>
<td>591934</td>
<td>3367921</td>
<td>11-May-06</td>
</tr>
<tr>
<td>Thistlethwaite WMA(^2)</td>
<td>8</td>
<td>593400</td>
<td>3392392</td>
<td>30-Apr-06</td>
</tr>
<tr>
<td>Bayou Teche NWR(^1)</td>
<td>9</td>
<td>649094</td>
<td>3291516</td>
<td>3-May-06</td>
</tr>
<tr>
<td>Evangeline Parish(^4)</td>
<td>10</td>
<td>573489</td>
<td>3419187</td>
<td>19-May-06</td>
</tr>
<tr>
<td>Three Rivers WMA(^2)</td>
<td>11</td>
<td>626036</td>
<td>3450043</td>
<td>25-May-06</td>
</tr>
<tr>
<td>Lake Fausse Pointe State Park(^1)</td>
<td>12</td>
<td>633844</td>
<td>3326000</td>
<td>11-Apr-06</td>
</tr>
<tr>
<td>Pointe Coupee Parish(^3)</td>
<td>13</td>
<td>618112</td>
<td>3416869</td>
<td>1-Apr-06</td>
</tr>
<tr>
<td>Iberville Parish(^4)</td>
<td>14</td>
<td>653831</td>
<td>3357290</td>
<td>22-Apr-06</td>
</tr>
<tr>
<td>St. Landry Parish(^4)</td>
<td>15</td>
<td>616342</td>
<td>3396503</td>
<td>17-May-06</td>
</tr>
<tr>
<td>Iberville Parish(^2)</td>
<td>16</td>
<td>661014</td>
<td>3337388</td>
<td>31-May-06</td>
</tr>
<tr>
<td>Lake Ophelia NWR(^1)</td>
<td>17</td>
<td>606957</td>
<td>3453062</td>
<td>23-May-06</td>
</tr>
<tr>
<td>Dewey M. Wills WMA(^2)</td>
<td>18</td>
<td>588384</td>
<td>3482763</td>
<td>15-Apr-06</td>
</tr>
<tr>
<td>St. Landry Parish(^4)</td>
<td>19</td>
<td>600438</td>
<td>3411519</td>
<td>18-May-06</td>
</tr>
<tr>
<td>St. Landry Parish(^3)</td>
<td>20</td>
<td>606248</td>
<td>3371224</td>
<td>6-May-06</td>
</tr>
<tr>
<td>Alligator Bayou(^3)</td>
<td>21</td>
<td>690648</td>
<td>3355476</td>
<td>1-Jun-06</td>
</tr>
<tr>
<td>Cypress Island(^3)</td>
<td>22</td>
<td>606253</td>
<td>3342910</td>
<td>26-Mar-06</td>
</tr>
</tbody>
</table>

UTM coordinates were calculated in the North American 1983 geographic coordinate system. NWR-National Wildlife Refuge (U.S. Fish and Wildlife Service), WMA-Wildlife Management Area (Louisiana Department of Wildlife and Fisheries), 1-government protected, 2-government multi-use land (including timber), 3-private, non-industry, 4-private, timber industry.
Appendix 2 – Fecundity, Juvenile Survival, and Adult Survival in Logs of Different Size and Adult Abundance from Chapter 3

a) Statistical Analysis

Because there were a high number of logs without larvae (7/29), the first response was split into two sub-analyses: a logistic regression predicting the probability of any offspring \( (P_b) \) and a linear regression predicting the number of young \( (B) \) after zeroes were removed. For all four analyses the log was the unit of replication. Predictor variables were log size (small or large) and number of females (categories 1, 2, 3). All combinations of variables were considered including an intercept only model (4 models).

b) Results

Table A2.1 Test of the hypothesis that the number of offspring per female in logs was dependent on conspecific density and log size.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>( \bar{x} )</th>
<th>( \sum w_i )</th>
<th>iR^2_n</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \beta_0 )</td>
<td>1.87 (0.25)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \beta_F )</td>
<td>2 -1.08 (0.35)</td>
<td>1.0</td>
<td>37.0%</td>
</tr>
<tr>
<td>( \beta_{dia} )</td>
<td>0.09 (0.11)</td>
<td>0.28</td>
<td>5.2%</td>
</tr>
</tbody>
</table>

b) Best model set

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>( \Delta AIC_c )</th>
<th>( w_i )</th>
<th>R^2_n</th>
</tr>
</thead>
<tbody>
<tr>
<td>F</td>
<td>3</td>
<td>0.00</td>
<td>0.72</td>
<td>38.7%</td>
</tr>
<tr>
<td>dia + F</td>
<td>2</td>
<td>0.845</td>
<td>0.35</td>
<td>42.2%</td>
</tr>
</tbody>
</table>

Only logs with one or more offspring present in September 2008 are included (n = 22). The response is the log-transformed number of larvae per female. \( \bar{x} \) = model-averaged regression coefficients (SE), \( \bar{z} \) = standardized regression coefficients (SE), \( \sum w_i \) = summed Akaike weight, iR^2_n = proportion of pseudo-R^2 independently explained by a variable in full model, jR^2_n = proportion of pseudo-R^2 jointly explained with other variables in full model (negative values indicate suppression), k = number of parameters in model, \( \Delta AIC_c \) = change in Akaike information criterion adjusted for small sample sizes, \( w_i \) = Akaike weight indicating probability that a model is the “true” one, R^2_n = Nagelkerke pseudo-R^2. F = number of females, dia = diameter class of log.
Table A2.2 Test of the hypothesis that juvenile survival from September to November 2008 was influenced by log size and/or conspecific adult density.

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\bar{x}$</th>
<th>$\sum w_i$</th>
<th>i$R^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\beta_0$</td>
<td>-0.54 (0.34)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_F$</td>
<td>2 -0.80 (0.44)</td>
<td>1.0</td>
<td>44.8%</td>
</tr>
<tr>
<td>$\beta_{dia}$</td>
<td>3 -1.23 (0.36)</td>
<td>0.54</td>
<td>6.3%</td>
</tr>
</tbody>
</table>

b) Best model set

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>$\Delta$AIC$^c$</th>
<th>$w_i$</th>
<th>R$^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>dia + F</td>
<td>4</td>
<td>0.00</td>
<td>0.54</td>
<td>51.1%</td>
</tr>
<tr>
<td>F</td>
<td>3</td>
<td>0.33</td>
<td>0.46</td>
<td>42.1%</td>
</tr>
</tbody>
</table>

Only logs with one or more offspring present in September 2008 are included (n = 21). The response is the proportion of larvae censused in September present as adults in November. $\bar{x}$ = model-averaged regression coefficients (SE), $\hat{z}$ = standardized regression coefficients (SE), $\sum w_i$ = summed Akaike weight, i$R^2_n$ = proportion of pseudo-R$^2$ independently explained by a variable in full model, j$R^2_n$ = proportion of pseudo-R$^2$ jointly explained with other variables in full model (negative values indicate suppression), k = number of parameters in model, $\Delta$AIC$^c$ = change in Akaike information criterion adjusted for small sample sizes, $w_i$ = Akaike weight indicating probability that a model is the “true” one, R$^2_n$ = Nagelkerke pseudo-R$^2$. F = number of females, dia = diameter class of log.
Table A2.3 Test of the hypotheses that adult survival from June to November 2008 was influenced by a) conspecific density and/or log size (n = 28 logs).

a) Model-averaged estimates

<table>
<thead>
<tr>
<th>Predictor</th>
<th>( \bar{x} )</th>
<th>( \sum w_i )</th>
<th>iR^2_n</th>
</tr>
</thead>
<tbody>
<tr>
<td>( \beta_0 )</td>
<td>0.69 (0.34)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>( \beta_F )</td>
<td>0.06 (0.14)</td>
<td>0.24</td>
<td>10.2%</td>
</tr>
<tr>
<td>( \beta_{dia} )</td>
<td>-0.29 (0.23)</td>
<td>0.39</td>
<td>4.02%</td>
</tr>
</tbody>
</table>

b) Best model set

<table>
<thead>
<tr>
<th>Model</th>
<th>k</th>
<th>( \Delta AIC_c )</th>
<th>( w_i )</th>
<th>( R^2_n )</th>
</tr>
</thead>
<tbody>
<tr>
<td>dia</td>
<td>2</td>
<td>0.000</td>
<td>0.39</td>
<td>9.0%</td>
</tr>
<tr>
<td>intercept only</td>
<td>1</td>
<td>0.142</td>
<td>0.37</td>
<td>0%</td>
</tr>
<tr>
<td>F</td>
<td>3</td>
<td>1.009</td>
<td>0.24</td>
<td>14.2%</td>
</tr>
</tbody>
</table>

The response is the proportion of adults censused in September present as adults in November. \( \bar{x} \) = model-averaged regression coefficients (SE), \( \hat{z} \) = standardized regression coefficients (SE), \( \sum w_i \) = summed Akaike weight, iR^2_n = proportion of pseudo-R^2 independently explained by a variable in full model, jR^2_n = proportion of pseudo-R^2 jointly explained with other variables in full model (negative values indicate suppression), k = number of parameters in model, \( \Delta AIC_c \) = change in Akaike information criterion adjusted for small sample sizes, \( w_i \) = Akaike weight indicating probability that a model is the “true” one, \( R^2_n \) = Nagelkerke pseudo-R^2. F = number of females, dia = diameter class of log.
Figure A2.1 Test of the influence of log diameter and conspecific density on *O. disjunctus* performance including: a) the probability larvae were present in a log in September (*n* = 29 logs). Logs varied in diameter (~9 cm, ~22 cm) and the number of females (1, 2, 3), but only diameter was an informative predictor of the presence of offspring; b) the number of larvae present in September (*n* = 22 logs, logs without larvae are excluded); c) the proportion of juveniles present in September which survived until November (*n* = 21 logs, logs without larvae are excluded). Values are back-transformed model-averaged estimates of least squares means with standard error bars. Variables are those deemed informative based on the AICc values of candidate models. Different letters indicate significant least squares differences among model-averaged means (*α* = 0.05).
Table A3.1 Pearson’s correlation among predictors.

<table>
<thead>
<tr>
<th></th>
<th>ant</th>
<th>trm</th>
<th>btl</th>
<th>wid</th>
<th>hol</th>
<th>dec</th>
<th>sz</th>
<th>sng</th>
<th>can</th>
<th>G</th>
<th>lev</th>
<th>for</th>
<th>frg</th>
</tr>
</thead>
<tbody>
<tr>
<td>ant</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>trm</td>
<td>0.02</td>
<td>1.00</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>btl</td>
<td>-0.05</td>
<td>-0.03</td>
<td>1.00</td>
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<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>wid</td>
<td>-0.02</td>
<td>0.09</td>
<td>0.02</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>hol</td>
<td>0.07</td>
<td>-0.02</td>
<td>-0.09</td>
<td>0.06</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>dec</td>
<td>0.14</td>
<td>-0.03</td>
<td>0.00</td>
<td>0.06</td>
<td>-0.03</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>sz</td>
<td>-0.07</td>
<td>0.06</td>
<td>0.04</td>
<td>0.62</td>
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<td>-0.06</td>
<td>1.00</td>
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</tr>
<tr>
<td>sng</td>
<td>-0.11</td>
<td>0.11</td>
<td>0.03</td>
<td>0.33</td>
<td>0.02</td>
<td>-0.07</td>
<td>0.14</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
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<td></td>
</tr>
<tr>
<td>can</td>
<td>-0.06</td>
<td>-0.01</td>
<td>0.01</td>
<td>0.07</td>
<td>-0.08</td>
<td>0.07</td>
<td>0.07</td>
<td>0.06</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
<td></td>
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<td>G</td>
<td>0.00</td>
<td>0.02</td>
<td>-0.02</td>
<td>-0.02</td>
<td>-0.01</td>
<td>-0.03</td>
<td>0.02</td>
<td>0.00</td>
<td>0.15</td>
<td>1.00</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>lev</td>
<td>0.02</td>
<td>0.03</td>
<td>0.00</td>
<td>0.05</td>
<td>0.05</td>
<td>0.02</td>
<td>0.03</td>
<td>0.10</td>
<td>-0.18</td>
<td>-0.20</td>
<td>1.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>for</td>
<td>-0.05</td>
<td>0.00</td>
<td>-0.01</td>
<td>0.04</td>
<td>0.03</td>
<td>0.07</td>
<td>0.02</td>
<td>0.03</td>
<td>0.47</td>
<td>0.06</td>
<td>-0.04</td>
<td>1.00</td>
<td></td>
</tr>
<tr>
<td>frg</td>
<td>0.03</td>
<td>-0.03</td>
<td>-0.03</td>
<td>-0.05</td>
<td>-0.01</td>
<td>0.10</td>
<td>-0.05</td>
<td>-0.10</td>
<td>-0.33</td>
<td>0.01</td>
<td>0.03</td>
<td>0.01</td>
<td>1.00</td>
</tr>
</tbody>
</table>

Bold values indicate significant correlation ($\alpha = 0.05$), shaded values are significant after a Bonferonni correction ($\alpha/78$). Variable abbreviations (see also Table 3.1): trm = termite, ant = ants, btl = other wood boring beetles, wid = diameter of log, hol = hollow log, dec = decay class, sz = number of territories per log, sng = snag (yes/no), can = % canopy cover, G = basal area of standing trees, lev = levee present, for = % forest cover within 225 ha, frg = fragmentation index.
Appendix 4 – Calculation of Connectivity to Conspecifics and Other Logs from Chapter 3

To model dependency on the distribution of conspecifics or resources, I calculated the connectivity function:

\[ C_i = \frac{\sum_{j \neq i} k(d_{ij})y_j}{\sum_{j \neq i} k(d_{ij})}, \]  \hspace{1cm} (A4.1)

where \( y_{ij} \) is the value describing the presence of conspecifics or suitable habitat at log \( j \) (see below), \( d_{ij} \) is the distance between logs \( i \) and \( j \), and \( k(d) \) is a two dimensional dispersal kernel described the exponential distribution such that

\[ k(d) = \frac{\alpha^2}{2\pi} e^{-\alpha d}, \]  \hspace{1cm} (A4.2)

where \( 1/\alpha \) indicates the average dispersal distance or the “dispersal neighborhood” (van Teeffelen and Ovaskainen 2007). An exponential distribution of dispersal distances assumes “fat-tailed” dispersal, or more long-distance dispersal than would be expected under a Gaussian distribution, a common phenomenon found in nature with important consequences for long-term connectivity among sites (Turchin 1998). The type of weighting function for a dispersal kernel appears to have little effect the outcome of a regression model and its optimization for the value of the neighborhood parameter \( \alpha \) is recommended (Dormann et al. 2007). I followed the optimization method of Oksanen (Oksanen 2004) to search the parameter space between 1 and 30 meters for the dispersal neighborhood that yielded the lowest AICc value when predicting incidence in combination with covariates described above, a method that helps to identify the scale at which population aggregation occurs (van Teeffelen and Ovaskainen 2007). This
resulting estimate is probably slightly larger than the average dispersal distance for individuals (van Teeffelen and Ovaskainen 2007).

To measure the influence of nearby conspecifics, the value $y_j$ was calculated as $y_j = p_j A_j$, where $p_j$ is the incidence ($0 = \text{empty log}, 1 = \text{conspecifics present}$), and $A_j$ is the area of log $j$. Similarly, resource distribution was modeled where $y_j = A_j$. The number of sections ($A_j$) of all logs were divided by the size of the smallest occupied patch so that units can be interpreted as the number of territories (Oksanen 2004). Note that my value of $y_j$ is different from the one used by van Teeffelen and Ovaskainen (2007) who did not include area. Instead, I included the size of neighboring logs to recognize that size is likely to influence the number of colonists from that site (Hanski 1994). The number of conspecifics in a nearby patch may also influence the attraction of an individual to a patch (Doligez et al. 2004), and these two hypotheses are not distinguished in this model. In the resource distribution model, the inclusion of $A_j$ acknowledges the fact that larger logs constitute more resources. Once the best model was selected, the covariates within that model were then analyzed using the model averaging process described previously.
Appendix 5 – Single-Level Analyses of Passalid Incidence from Chapter 3

Table A5.1 Variable selection at a single hierarchical level (log-section).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\bar{x}$</th>
<th>$\hat{z}$</th>
<th>$\sum w_i$</th>
<th>$iR^2_n$</th>
<th>$jR^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Proportion of log-sections occupied by passalids</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>-2.98 (0.34)</td>
<td>0.11</td>
<td>0.23</td>
<td>0.9%</td>
<td>-0.8%</td>
</tr>
<tr>
<td>$\beta_{trm}$</td>
<td>0.03 (0.05)</td>
<td>-0.38</td>
<td>1.00</td>
<td>1.8%</td>
<td>-1.5%</td>
</tr>
<tr>
<td>$\beta_{ant}$</td>
<td>-0.39 (0.16)</td>
<td>0.22</td>
<td>0.52</td>
<td>2.5%</td>
<td>-1.8%</td>
</tr>
<tr>
<td>$\beta_{btl}$</td>
<td>0.14 (0.10)</td>
<td>-0.47</td>
<td>1.00</td>
<td>2.7%</td>
<td>-1.3%</td>
</tr>
<tr>
<td>$\beta_{hol}$</td>
<td>-0.75 (0.32)</td>
<td>0.15</td>
<td>0.29</td>
<td>2.4%</td>
<td>-2.3%</td>
</tr>
<tr>
<td>$\beta_{wid}$</td>
<td>0.04 (0.04)</td>
<td>1.84</td>
<td>1.00</td>
<td>2.5%</td>
<td>-2.0%</td>
</tr>
<tr>
<td>$\beta_{dec}$</td>
<td>2.10 (0.30)</td>
<td>1.00</td>
<td>1.00</td>
<td>2.5%</td>
<td>-2.0%</td>
</tr>
<tr>
<td>3</td>
<td>1.88 (0.29)</td>
<td>1.84</td>
<td>1.00</td>
<td>2.5%</td>
<td>-2.0%</td>
</tr>
<tr>
<td>b) Best model set</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>ant+btl+dec+hol</td>
<td>7</td>
<td>0.00</td>
<td>0.25</td>
<td>12.6%</td>
<td>0.69</td>
</tr>
<tr>
<td>ant+hol+dec</td>
<td>6</td>
<td>0.13</td>
<td>0.23</td>
<td>12.4%</td>
<td>0.68</td>
</tr>
<tr>
<td>ant+btl+dec+hol+wid</td>
<td>8</td>
<td>1.03</td>
<td>0.15</td>
<td>12.8%</td>
<td>0.70</td>
</tr>
<tr>
<td>ant+dec+hol+wid</td>
<td>7</td>
<td>1.18</td>
<td>0.14</td>
<td>12.5%</td>
<td>0.69</td>
</tr>
<tr>
<td>trm+ant+btl+dec+hol</td>
<td>8</td>
<td>1.41</td>
<td>0.12</td>
<td>12.7%</td>
<td>0.69</td>
</tr>
<tr>
<td>trm+ant+dec+hol</td>
<td>7</td>
<td>1.63</td>
<td>0.11</td>
<td>12.4%</td>
<td>0.69</td>
</tr>
</tbody>
</table>

Variables with Akaike weights of 0.5 or greater were retained for multi-level analysis. $\bar{x}$ = model-averaged regression coefficients (SE), $\hat{z}$ = standardized regression coefficients (SE), $\sum w_i$ = summed Akaike weight, $iR^2_n$ = proportion of pseudo-$R^2$ independently explained by a variable in full model, $jR^2_n$ = proportion of pseudo-$R^2$ jointly explained with other variables in full model (negative values indicate suppression), $k$ = number of parameters in model, $\Delta AIC_c$ = change in Akaike information criterion adjusted for small sample sizes, $w_i$ = Akaike weight indicating probability that a model is the “true” one, $R^2_n$ = Nagelkerke pseudo-$R^2$. Variable abbreviations are found in Table 3.1.
### Table A5.2 Variable selection at a single hierarchical level (log).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\bar{x}$</th>
<th>$\hat{z}$</th>
<th>$\sum w_i$</th>
<th>$iR^2_n$</th>
<th>$jR^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Proportion of log-sections in a log occupied by passalids</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>-2.03 (0.15)</td>
<td>-1.65 (0.09)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_{sz}$</td>
<td>0.38 (0.23)</td>
<td>0.78 (0.16)</td>
<td>1.0</td>
<td>4.8%</td>
<td>-0.2%</td>
</tr>
<tr>
<td>$\beta_{sng}$</td>
<td>-0.75 (0.35)</td>
<td>-0.46 (0.21)</td>
<td>1.0</td>
<td>0.8%</td>
<td>-0.2%</td>
</tr>
<tr>
<td>b) Best model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$k$</td>
<td>$\Delta AIC_c$</td>
<td>$w_i$</td>
<td>$R^2_n$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>sz+sng</td>
<td>3</td>
<td>0.00</td>
<td>1.0</td>
<td>5.6%</td>
<td></td>
</tr>
</tbody>
</table>

Variables with Akaike weights of 0.5 or greater were retained for multi-level analysis. $\bar{x}$ = model-averaged regression coefficients (SE), $\hat{z}$ = standardized regression coefficients (SE), $\sum w_i$ = summed Akaike weight, $iR^2_n$ = proportion of pseudo-$R^2$ independently explained by a variable in full model, $jR^2_n$ = proportion of pseudo-$R^2$ jointly explained with other variables in full model (negative values indicate suppression), $k$ = number of parameters in model, $\Delta AIC_c$ = change in Akaike information criterion adjusted for small sample sizes, $w_i$ = Akaike weight indicating probability that a model is the “true” one, $R^2_n$ = Nagelkerke pseudo-$R^2$. Variable abbreviations are found in Table 3.1.

### Table A5.3 Variable selection at a single hierarchical level (subplot).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\bar{x}$</th>
<th>$\hat{z}$</th>
<th>$\sum w_i$</th>
<th>$iR^2_n$</th>
<th>$jR^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Proportion of log-sections in a subplot occupied by passalids</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>-2.03 (0.15)</td>
<td>-1.47 (0.08)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_{can}$</td>
<td>0.38 (0.08)</td>
<td>-0.28 (0.16)</td>
<td>0.77</td>
<td>4.0%</td>
<td>0.3%</td>
</tr>
<tr>
<td>$\beta_{G}$</td>
<td>-0.75 (0.35)</td>
<td>-0.11 (0.16)</td>
<td>0.23</td>
<td>0.9%</td>
<td>0.3%</td>
</tr>
<tr>
<td>b) Best model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$k$</td>
<td>$\Delta AIC_c$</td>
<td>$w_i$</td>
<td>$R^2_n$</td>
<td></td>
<td></td>
</tr>
<tr>
<td>can</td>
<td>2</td>
<td>0.00</td>
<td>0.54</td>
<td>4.3%</td>
<td></td>
</tr>
<tr>
<td>can+G</td>
<td>3</td>
<td>1.62</td>
<td>0.24</td>
<td>4.9%</td>
<td></td>
</tr>
<tr>
<td>intercept only</td>
<td>1</td>
<td>1.73</td>
<td>0.23</td>
<td>0.0%</td>
<td></td>
</tr>
</tbody>
</table>

Variables with Akaike weights of 0.5 or greater were retained for multi-level analysis. $\bar{x}$ = model-averaged regression coefficients (SE), $\hat{z}$ = standardized regression coefficients (SE), $\sum w_i$ = summed Akaike weight, $iR^2_n$ = proportion of pseudo-$R^2$ independently explained by a variable in full model, $jR^2_n$ = proportion of pseudo-$R^2$ jointly explained with other variables in full model (negative values indicate suppression), $k$ = number of parameters in model, $\Delta AIC_c$ = change in Akaike information criterion adjusted for small sample sizes, $w_i$ = Akaike weight indicating probability that a model is the “true” one, $R^2_n$ = Nagelkerke pseudo-$R^2$. Variable abbreviations are found in Table 3.1.
Table A5.4 Variable selection at a single hierarchical level (plot).

<table>
<thead>
<tr>
<th>Predictor</th>
<th>$\bar{x}$</th>
<th>$\hat{z}$</th>
<th>$\sum w_i$</th>
<th>$iR^2_n$</th>
<th>$jR^2_n$</th>
</tr>
</thead>
<tbody>
<tr>
<td>a) Proportion of log-sections in a plot occupied by passalids</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\beta_0$</td>
<td>-3.76 (0.45)</td>
<td>-1.62 (0.09)</td>
<td>1.0</td>
<td>45.9%</td>
<td>40.8%</td>
</tr>
<tr>
<td>$\beta_{\text{lev}}$</td>
<td>2.07 (0.43)</td>
<td>1.40 (0.30)</td>
<td>1.0</td>
<td>12.2%</td>
<td>23.1%</td>
</tr>
<tr>
<td>$\beta_{\text{for}}$</td>
<td>0.17 (0.09)</td>
<td>0.14 (0.32)</td>
<td>0.8</td>
<td>9.7%</td>
<td>20.5%</td>
</tr>
<tr>
<td>$\beta_{\text{frg}}$</td>
<td>0.02 (0.01)</td>
<td>0.10 (0.22)</td>
<td>0.3</td>
<td>27.0%</td>
<td>43.1%</td>
</tr>
<tr>
<td>$\beta_{\text{forXfrg}}$</td>
<td>0.00 (0.00)</td>
<td>0.54 (0.34)</td>
<td>0.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>b) Best model</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>$\text{lev+for+frg}$</td>
<td>4</td>
<td>0.00</td>
<td>0.48</td>
<td>94.1%</td>
<td></td>
</tr>
<tr>
<td>$\text{lev+for+frg+forXfrg}$</td>
<td>5</td>
<td>0.81</td>
<td>0.32</td>
<td>94.8%</td>
<td></td>
</tr>
<tr>
<td>$\text{lev+for}$</td>
<td>3</td>
<td>1.69</td>
<td>0.21</td>
<td>92.7%</td>
<td></td>
</tr>
</tbody>
</table>

Variables with Akaike weights of 0.5 or greater were retained for multi-level analysis.  $\bar{x}$ = model-averaged regression coefficients (SE),  $\hat{z}$ = standardized regression coefficients (SE),  $\sum w_i$ = summed Akaike weight,  $iR^2_n$ = proportion of pseudo-$R^2$ independently explained by a variable in full model,  $jR^2_n$ = proportion of pseudo-$R^2$ jointly explained with other variables in full model (negative values indicate suppression),  $k$ = number of parameters in model,  $\Delta AIC_c$ = change in Akaike information criterion adjusted for small sample sizes,  $w_i$ = Akaike weight indicating probability that a model is the “true” one,  $R^2_n$ = Nagelkerke pseudo-$R^2$. Variable abbreviations are found in Table 3.1.
Appendix 6 – Dispersal Neighborhood Optimization from Chapter 3

Figure A6.1 Optimization of dispersal neighborhood estimates. Dispersal neighborhood is the distance from which conspecific proximity (filled circles) or log proximity (open squares) is associated with incidence in a log. The optimized values were $\Delta AIC_c$ values calculated from general linear models predicting *O. disjunctus* occupancy in a 6.25 ha plot. Models differed only in which proximity metric was used: conspecific proximity (filled circles) or resource proximity (open squares). Other predictors included log size, decay class, log position, physical slope, and x,y coordinates of each log.
Appendix 7 – Copyright Permission for Chapter 2

from Alan Kahan <akahan@entsoc.org>
to hjacks1@lsu.edu
date Sun, Aug 1, 2010 at 4:34 PM
subject RE: copyright permission

July 30, 2010

Heather Bird Jackson
PhD candidate
Department of Biological Sciences
Louisiana State University
107 Life Sciences Building
Baton Rouge, LA 70803

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Fax: 301-731-4538
akahan@entsoc.org
Vita

Heather Bird Jackson was born in the Mojave Desert of Ridgecrest, California, on September 17, 1978, but spent most of her childhood in metropolitan Denver, Colorado, where the Rocky Mountains meet the Great Plains. Given the example of her father, an atmospheric physicist who made his living in the pursuit of knowledge, and the encouragement of Joe Otero, who improved the lives of many as a high school math teacher, Heather studied biology education as an undergraduate at Brigham Young University where she was made constantly aware of the awe-inspiring natural world by the Wasatch Front which rose 1600 m above campus. After teaching science to middle school children for three years, Heather returned to Brigham Young University in 2003 to study lichen ecology with Dr. Larry St. Clair. She subsequently studied dispersal ecology with Dr. Jim Cronin at Louisiana State University in the lower Mississippi river alluvial floodplain. Heather maintains a passion for the natural world and for expanding the minds of young people.