

# Mechanisms driving the density–area relationship in a saproxylic beetle

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Received: 2 March 2013 / Accepted: 28 May 2013 / Published online: 29 June 2013  
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**Abstract** Mechanisms underlying density–area relationships (correlations between population density and patch size) have rarely been tested experimentally. It is often assumed that higher density on large patches is evidence that large patches are high quality (i.e. have greater survival and reproduction), but the same pattern could result from disproportionate movement from small to large patches. Movement-based and within-patch processes must be experimentally separated to show that large patches are indeed of higher quality, but few studies have done so. We experimentally tested movement-based and within-patch hypotheses to explain the positive density–area relationship observed for a saproxylic (decayed wood-dependent) beetle, *Odontotaenius disjunctus* Illiger (Coleoptera: Passalidae). In separate experiments we quantified (1) immigration into and (2) finite growth rate within logs (=patches) that varied in size and density of conspecific beetles. A log was 11.7-fold [95 % confidence interval (CI) 3.4–40.8] and 10.5-fold (95 % CI 2.7–40.9) more likely to contain a new immigrant if it was large or contained a conspecific pair

of beetles, respectively. Neither log size nor conspecific density was associated with changes in finite growth rate that would lead to higher density: decreased log size and increased conspecific density reduced finite growth rate in direct proportion to the loss in available resources per mating pair. We conclude that movement behavior rather than habitat quality is responsible for the positive density–area relationship for *O. disjunctus*. An important implication of our results is that population density is an imperfect indicator of habitat quality.

**Keywords** Patch size effect · Habitat selection · Allee effect · Aggregation · Social information

## Introduction

Although habitat amount alone can account for the density of many species (Fahrig 2003), some species are also influenced by the configuration (or fragmentation) of habitat (Donovan and Lamberson 2001). The population density of some species, for example, may be sensitive to patch size, resulting in a positive or negative density–area relationship (also called the patch-size effect). Although density–area relationships are well described for many taxa (Bender et al. 1998; Bolger et al. 2008; Bowers and Matter 1997; Connor et al. 2000; Hambäck et al. 2007), the mechanisms underlying these patterns are not. An understanding of the mechanisms causing density–area relationships is important to the development of appropriate conservation plans (Ahlering et al. 2010) and will improve predictions of species distributions. Density–area relationship hypotheses can be divided into movement-based and within-patch hypotheses, depending on whether the important underlying mechanisms are associated with the movement of individuals in

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Communicated by Roland Brandl.

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**Electronic supplementary material** The online version of this article (doi:10.1007/s00442-013-2697-5) contains supplementary material, which is available to authorized users.

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and out of patches or the birth and death processes within patches, respectively (Connor et al. 2000).

Understanding density–area relationships is complicated by the fact that movement-based and within-patch hypotheses are not mutually exclusive. In fact, movement behavior (especially habitat preference) is expected to be linked to predicted within-patch fitness, a notion that underlies the ideal free distribution (Fretwell and Lucas 1969). However, within-patch fitness is not the only selective force acting on movement behavior. Dispersal itself is a costly endeavor, representing an increased risk of mortality and a reproductive cost due to the time and energy spent on movement (Burgess et al. 2012; Daniels and Walters 2000; Roff 1977). The acceptance of suboptimal habitat is expected to be selected for if the cost of further dispersal is large (Stamps 2001). Furthermore, if habitat quality is difficult to assess at the time of settlement, movement decisions may be based on imperfect (“proximate”) indicators of habitat quality (Stamps 2001), such as the presence or density of conspecifics (Danchin et al. 2004). Dispersal costs and imperfect information can lead to habitat selection that is not well correlated with habitat quality. Movement-based and within-patch hypotheses should therefore be tested separately in order to determine if cues used during movement correspond to within-patch processes (Stamps 2001).

Studies of the mechanisms responsible for density–area relationships have been to date predominantly correlational (e.g. Hambäck et al. 2007; Östman et al. 2009). To our knowledge, only seven studies have attempted to experimentally assess the mechanisms underlying density–area relationships, and all but two focused exclusively on movement-based hypotheses (Table 1). These studies found support for the role of movement in positive density–area relationships, but with one exception (Cronin et al. 2004) did not experimentally test whether movement was associated with within-patch fitness.

We experimentally tested movement-based and within-patch hypotheses that might explain the positive density–area relationship observed for a saproxylic (decayed wood-dependent) beetle, *Odontotaenius disjunctus* Illiger (Coleoptera: Passalidae) (Fig. 3b in Jackson et al. 2012). We monitored beetle movement and reproduction within outdoor experimental landscapes containing logs of two sizes and with different densities of resident beetles. We tested two movement-based processes that could lead to a positive-density area relationship: beetles immigrate into large patches at a rate disproportionate to the increased resource availability per beetle (large log attraction, H3 and H5, Table 2), and/or beetles immigrate into patches with conspecifics more than would be expected given the decrease in resource availability per beetle (conspecific

**Table 1** Experimental studies testing mechanisms underlying a density–area relationship

Study	Organism	Density–area relationship <sup>a</sup>	Mechanisms underlying density–area relationship
Batch (1984)	Chrysomelid beetle ( <i>Acalymma innubum</i> ) on host plant ( <i>Cayaponia americana</i> )	Positive	Beetles stayed on large patches longer
Cronin (2003)	Planthopper ( <i>Prokelisia crocea</i> ) on host plant ( <i>Spartina pectinata</i> )	Positive	None found; density of immigrants unrelated to patch size
Cronin et al. (2004)	Planthopper ( <i>Prokelisia crocea</i> ) on host plant ( <i>Spartina pectinata</i> )	Positive	Movement out of (but not mortality within) patches increased with spider density, which have greater density in small patches
Finn and Giller (2000)	Various dung beetle species on dung pads	Positive	Density and residence time of colonizing beetles were greater on large pads. Larval density was also greater, but it is unclear if this is due to more colonizing adults and/or more productive adults
Fletcher (2009)	Least flycatchers	Positive	Flycatchers settled in small patches that they would otherwise not inhabit when conspecific calls were broadcast from them. Observations of vegetation quality and nest predation did not vary with patch size
Kareiva (1985)	Flea beetles ( <i>Phyllotreta cruciferae</i> and <i>P. striolata</i> ) in collard patches	Positive	Immigration increased slightly and emigration decreased strongly with patch size
Matter (1997)	Red milkweed beetles ( <i>Tetraopes tetraophthalmus</i> ) on host plant	Positive	Immigration per unit area was lower but beetles stayed longer on large patches

<sup>a</sup> A density–area relationship refers to the slope (positive or negative) of the relationship between density and patch size

**Table 2** Hypotheses explaining the positive density–area relationship for *Odontotaenius disjunctus*

Hypothesis	Statistical model <sup>a</sup>	Verbal hypothesis	Resulting density–area relationship
H1	Intercept only	There is no difference among logs	Negative or neutral (Bowman et al. 2002; Fletcher 2006)
H2	WOOD	The surface area of wood per potential pair dictates a beetle's response to a log	
H3	WOOD + LG	Log size increases immigration/growth rate even after accounting for resource availability	Positive if LG and/or CON are positive (Fletcher 2006), otherwise negative
H4	WOOD + CON <sup>b</sup>	The number of conspecifics increases immigration/growth rate after accounting for their negative effect on resource availability	
H5	WOOD + LG + CON	Log size and the number of conspecifics increase immigration/growth rate even after accounting for resource availability	

<sup>a</sup> Coefficients: WOOD, log-transformed surface area per beetle with fixed coefficient of 1; LG, log size; CON, abundance of conspecifics

<sup>b</sup> Conspecific abundance had four levels in the movement analyses: none, single beetle of the opposite sex, one pair, two pairs. In the growth rate analyses, the levels for conspecific abundance were 1, 2, and 3 pairs

attraction, H4, H5, Table 2). Similarly, we tested two within-patch processes: the increase in finite growth rate in large logs is disproportionate to the increase in resource availability (i.e. large patches are of higher quality, H3 and H5, Table 2) and/or finite growth rate is greater in the presence of conspecifics than would be expected given the decrease in resource availability per beetle (social facilitation, H4, H5, Table 2). Using these datasets we were able to draw conclusions about which process (immigration or reproductive success) contributes more to the positive density–area relationship, and whether immigration behavior is associated with expected reproductive success.

## Materials and methods

### Study species

Particularly abundant in the southern part of its range (i.e. most of the eastern USA; Schuster 1978), *O. disjunctus* is prominent as both a food source (e.g. in a study of the Florida black bear, passalids were the bear's main source of protein; Brown 2004) and as a major player in hardwood decay. Furthermore, *O. disjunctus* has a number of traits relevant to this study. Ground-moving, slow, and large (approx. 32 mm long), *O. disjunctus* has movements that are easy to observe (Jackson et al. 2009). Decayed hardwood provides both food and a year-round habitat for *O. disjunctus* (Gray 1946; Jackson et al. 2009; Pearse et al. 1936), making patch boundaries meaningful and easy to define. As *O. disjunctus* is one of only a few temperate passalid species, the time during which movement and larval development can optimally take place is restricted to warm summer months. Very few adults are found outside of logs except

during late spring or early fall (Jackson et al. 2009) when they are presumably searching for a new habitat. Adults are expected to settle quickly because galleries must be created for offspring which then take 3 warm months to develop from egg to adult (Gray 1946). *O. disjunctus* appears to be long-lived (at least one adult has been recaptured after 2 years; Gray 1946), and most adults were expected to survive during the breeding season (i.e. the length of our study). Like many birds which have shown complex habitat selection behaviors, mating *O. disjunctus* pairs share offspring care (Schuster and Schuster 1985), and their acoustic signals are associated with various conspecific interactions, such as mating and territory defense (Schuster 1983). Furthermore, members of Passalidae respond to conspecific olfactory cues (e.g. by repairing disturbed pupal cases; Valenzuela-González 1993). Previous to this study, however, all documented interactions have been confined to within a small experimental space. Males and females are similarly sized (Gray 1946) and have exhibited little difference in movement (Jackson et al. 2009) and aggressive behavior (males are slightly more aggressive; Schuster 1983) in previous studies, leading us to expect that males and females would behave similarly in our study.

### Experimental design

Two experiments were conducted in order to test the effects of patch size and conspecific density on immigration (a movement-based process) and post-settlement growth rate (a within-patch process). Our experiments were conducted in a bottomland hardwood forest in Baton Rouge, Louisiana, USA. Dominant trees in these forests include *Nyssa* spp. (tupelo), *Liquidambar styraciflua* L. (sweetgum), *Quercus* spp. (oak), and *Taxodium* spp. (cypress).

## Immigration

In the first experiment we measured the effect of patch size and conspecific density on two sequential responses: (1) the probability of visitation (presence on a patch 12 min after release) and (2) the likelihood of settlement (i.e. presence on a patch 1 week after release). The probability of visiting a patch was measured by observing the movement of beetles placed 0.5 m from a log. This distance was selected to ensure that beetles could perceive the log. In previous trials, beetles did not respond to a log that was >1 m away (Jackson 2010). This outcome indicates the willingness of a beetle to spend time and energy visiting a potential habitat. Attraction to conspecifics can be based on the direct benefits of conspecifics, such as mate availability (Allee 1927) or protection from predators (Nelson and Jackson 2008). Conspecifics may provide indirect benefits when they reduce search time (Fletcher 2006) or act as proximate cues of habitat quality (Calabuig et al. 2008; Stamps 1988). We included a treatment with single beetles of the opposite sex so that mate attraction could be compared to more general conspecific attraction. “Resident” beetles were either single beetles of the opposite sex to the “visitor” or were beetle pairs. Because the willingness to visit a patch may not indicate a final settlement decision, we returned to experimental logs 1 week later to see whether any non-resident beetles (i.e. beetles released near the log or beetles from other logs) were present in the log (methods are described below). We also kept track of how many resident beetles remained in the log.

We created experimental logs of equal length (40 cm) but different diameters (small: range 7–11 cm, approx. 11.3 dm<sup>2</sup> surface area; large: range 16–28 cm, approx. 27.7 dm<sup>2</sup> surface area) from two red oaks (*Quercus* sp.). The lengths of the experimental logs (and therefore the perimeter) were equal so that random movement would not lead to a pattern even though in nature, where large diameter logs are usually longer, random movement is expected to lead to a neutral or negative density–area relationship (Bowman et al. 2002). The oaks had fallen at the same time (Hurricane Katrina, 29 Aug 2005) and were in between decay classes 2 and 3 (i.e. sapwood was soft and could often be torn apart; Woodall and Williams 2005). These decay classes had the highest occupancy rate in field surveys (Jackson et al. 2012). The smallest logs were purposely selected to have less surface area than any log occupied in previous surveys (smallest occupied log 26.0 dm<sup>2</sup>; Jackson 2010) in order to test (1) whether beetle absence in small logs is due to choice and (2) if small logs are less preferred, could attraction to conspecifics override aversion to small log size. In order for us to inspect beetle galleries repeatedly without further damaging the log or harming the inhabitants, we modified logs following a procedure from

Hernandez-Martinez and Castillo (2003). Each log was cut longitudinally into 3-cm-thick sections, and the sections were held together with rubber tubing to form a complete log.

Experimental logs were placed in two plots, one in Louisiana State University’s Burden Research Plantation and the other in Louisiana State University’s Central Research Station. Logs were placed in 38-L plastic bins to prevent the emigration or immigration of beetles before the trials began (in cm: 50 long by 12 wide by 33 high). To help retain moisture, we lined the bottom of each bin with a 2-cm-thick layer of newspaper. Bins had 7-cm-diameter holes in the top covered with a screen to allow ventilation, and small 6.4-mm drainage holes were drilled in the bottom. Logs were placed in a grid with 6 m between each log and its nearest neighbor, a distance selected to minimize detection of nearby logs (logs of this size are not detected from 3 m away; Jackson 2010). All naturally occurring woody debris with a diameter of >5 cm was removed from the plots.

Large logs had approximately twice the surface area of small logs, so we placed twice as many beetles in large logs to keep densities comparable. The abundances of beetles in small logs were zero residents ( $n = 38$ ), a single beetle of the opposite sex to the visitor ( $n = 11$ ), and one male/female pair ( $n = 10$  logs). In large logs the densities were zero residents ( $n = 39$  logs), one male/female pair ( $n = 10$  logs), and two male/female pairs ( $n = 10$  logs). Resident beetles were collected from the surrounding forest and randomly assigned to logs. Before placement, the thoraces of beetles were marked with scratches using an insect pin such that they could be individually identified (Gray 1946).

Visiting beetles, which were collected and marked in the same way as resident beetles, were used in experimental trials within 1 day of capture. Before a trial was initiated, a log was removed from its bin and placed on the forest floor. The visitor was placed 0.5 m away from the log, close enough to allow perception of the log (Jackson 2010). To prevent agitation dispersal (rapid movement in response to handling; Turchin 1998) on the part of the visitor, we set the beetle’s container on its side and allowed the beetle to exit the container on its own (this took an average of 4.5 min). Once out of the container, the beetle was observed for 12 min (longer observation for up to 2 h indicated no change in the initial decision). If at the end of 12 min the beetle was on or under the log, the beetle was considered to have visited the log.

After the 12-min trial was complete, we left the logs exposed for 1 week to be settled by new beetles (i.e., the test visitors, residents from other logs, and in two cases, new beetles from outside the plot). Each log was then carefully taken apart, one section at a time, and the identities and locations of beetles were recorded. The quantities of

interest were the probability that a log was settled by a new individual and the probability that a log would retain one or more original resident(s).

In order to increase sample size, both phases of the experiment were conducted twice, once in May 2008 and once in June 2008. Fifty-two logs were tested in the first trial and 66 logs were used in the second trial.

#### *Finite growth rate*

In the second experiment, we measured the effect of log size and conspecific density on post-dispersal reproductive success. This experiment was performed at Louisiana State University's Central Research Station between June and November 2008 (long enough for juveniles to mature to adulthood). We measured finite population growth rate as the ratio of the number of adults in November (when all surviving offspring have reached adulthood) to the number of adults released in June (before offspring were present). The logs were the same ones used in the settlement experiment, but new beetles collected from the surrounding forest were randomly assigned to logs at abundances of one (6 small and 6 large logs), two (6 small and 6 large logs), or three male/female pairs (6 large logs). We placed beetles and logs in bins on 20 June 2008 and left the bins undisturbed after the experiment began except for two censuses, one at 80 days and the other at 157 days. The first census was timed to be able to count larvae, and the timing of the second census allowed offspring sufficient time to mature to adulthood. Two bins were damaged during Hurricane Gustav (1 September 2008) and were not included in the analysis of population growth.

#### Statistical analyses

We evaluated the information value of log size and the abundance of conspecifics when predicting the movement behavior of *O. disjunctus* by comparing five binomial logistic regression models, each based on a hypothesis concerning the mechanisms underlying a positive density–area relationship (H1–H5, Table 2). Analyzed in separate analyses, response variables included three measures associated with movement: (1) the tendency for beetles to visit logs (response = visitor is on log after 12 min), (2) the probability a log contained at least one permanent immigrant (response = a new beetle is in the log after 1 week), and (3) the probability a log retained at least one original resident after 1 week. One log was removed from immigration (2) and resident (3) analyses because it was infested with fire ants. Only those logs that contained residents at the beginning of the week were used in the resident (3) analysis [ $n = 118$  in (1) and (2), but  $n = 40$  in (3)].

Because we were interested in whether the effect of log size and conspecifics was different than would be expected based on resource availability, we explicitly accounted for resource availability per beetle in our statistical models (H2–H5, Table 2). If resource availability alone was important, then the positive effects of log size and the negative effects of additional beetles on resource availability could be accounted for with one measure: surface area of wood per beetle (“WOOD” in Table 2). If log size and/or conspecifics had an additional (and according to our expectations, positive) effect on beetle settlement, we expected log size and/or the number of conspecifics to be included in the best models along with resource availability. We measured resource availability as the surface area of wood divided by the number of original beetles, including the visiting beetle, in immigration analyses [ $\ln(\text{surface area}/\text{number of original beetles})$ ]. The natural log of resource availability was included in each model as an offset with a fixed effect size of 1, corresponding to the hypothesis that the odds of the response (visitation, settlement, or residency) are directly proportional (1:1) with resource availability.

We checked the adequacy of binomial regression models using two measures: the Wald–Wolfowitz runs test and the area under the receiver operating characteristic curve (AUC). We used the Wald–Wolfowitz runs test to evaluate whether residuals were binomially distributed and independent. For each binomial regression model, we simulated 100 datasets by drawing from a binomial distribution with predicted values equal to the model's linear predictors. Simulated data were re-analyzed using binomial regression. The resulting residuals were sorted in order of increasing fitted values and were labeled as either greater than or less than their associated fitted values (see Wood 2006, pg. 115). A Wald–Wolfowitz statistic was calculated for the residuals of each simulated dataset, and the resulting distribution of Wald–Wolfowitz statistics was compared to the Wald–Wolfowitz statistic for the empirical residuals. An empirical statistic within the 2.5 and 97.5 percentiles of the simulated statistics would indicate that our data are binomially distributed and independent. AUC indicates predictive accuracy where 0.5 indicates prediction as good as random and 1 indicates perfect prediction.

For reproductive success, we measured finite growth rate. To meet the assumption of normality, finite growth rate was  $\ln$ -transformed [ $\ln(N_{\text{Nov}}N_{\text{Sept}}^{-1} + 0.5)$ ]. As with the settlement analyses, resource availability was included in most models (H2–H5, Table 2) with a fixed coefficient of 1 corresponding to the hypothesis that growth rate and resource availability per beetle (also  $\ln$ -transformed) are directly proportional. Analysis of other responses related to within-patch fitness (fecundity, juvenile survival, adult survival, juvenile body size) is reported in Appendix A of the Electronic Supplementary Material (ESM). For all

response variables, we used the Akaike information criterion corrected for small sample size (AICc) to weight the importance of models.

## Results

### Immigration

Beetle response to conspecifics during visitation was consistent with conspecific attraction (H4 and H5 were most informative; Fig. 1a; Table 3—Probability that a beetle visited a log within 0.5 m of release). The following results are from the full model (H5). After controlling for the change in surface area per beetle, the presence of a beetle of the opposite sex, a single beetle pair, and two beetle pairs increased the odds of visiting a log by 23.2-fold

[confidence interval (CI) 2.7–198.5-, 6.5-fold (CI 2.0–20.9), and 14.5-fold (CI 1.6–128.1), respectively, relative to an empty log with the same surface area per beetle. The presence of a potential mate increased the odds of visitation relative to the presence of a single pair by 3.6-fold (CI 0.3–36.5).

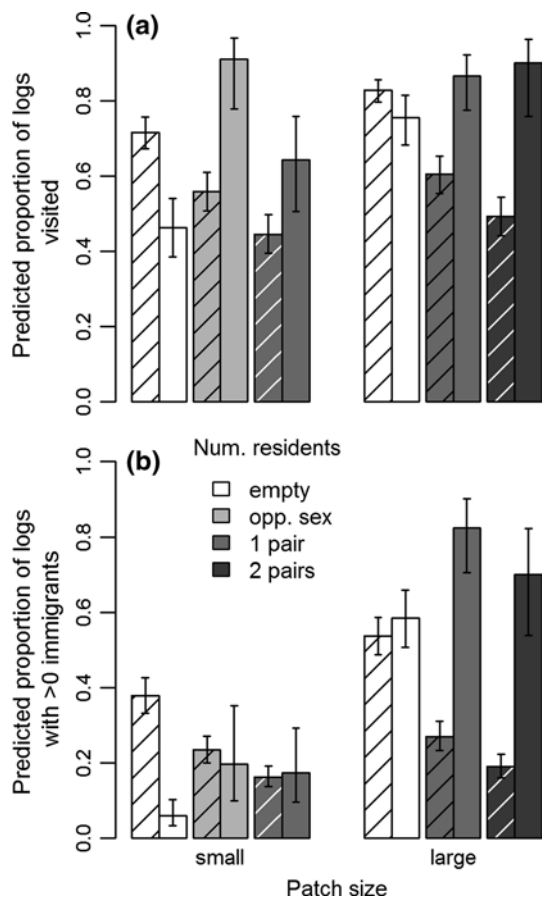
Beetles were clearly able to distinguish between small- and large-diameter logs during visitation, and there was weak evidence that this attraction to large logs was greater than expected given the increase in surface area per beetle (H4 and H5 were the most informative models; Fig. 1a; Table 3—Probability that a log contained at least one immigrant a week after it was colonized). The odds of visiting a log were increased by 1.9-fold (CI 0.8–4.6) relative to a small log with the same surface area per beetle.

Settlement of logs by immigrant beetles mirrored our findings for visitation, except that evidence for large log attraction was much stronger (H5 was most informative model; Fig. 1b; Table 3—Probability that a log contained at least one immigrant a week after it was colonized). After controlling for the change in surface area per beetle, new beetles were 11.7-fold more likely to settle in a large log than in a small log (CI 3.4–40.8; Fig. 1b; Table 3—Probability that a log contained at least one immigrant a week after it was colonized). The odds of settlement in a log increased dramatically if residents were present in a log at the beginning of the experiment, with no apparent difference among conspecific treatments (single beetle: +7.7x, CI 1.1–53.9; 1 pair: +10.5x, CI 2.7–40.9; 2 pairs: +8.2x, CI 1.8–36.2; Fig. 1b; Table 3—Probability that a log contained at least one immigrant a week after it was colonized).

Less than half of the experimental logs contained an original resident at the end of a week. The proportion of logs containing at least one of the original residents increased with log size and number of conspecifics (small, opposite sex 0.1; small, one pair 0.1; large, one pair 0.2, large, two pair 0.5), but the model that best represented this pattern was highly uncertain ( $\Delta$ AICc between best and worst model 2.47; Table 3—Probability that a log retained at least one of its original residents after being exposed for 1 week).

### Finite growth rate

Resource availability positively influenced growth rate, and there was little evidence for an additional effect of log size or conspecifics on growth rate (H2 model was most informative; Table 3—Finite growth rate in a log after one reproductive season; Fig. 2). If anything, the additional effects of log size and conspecific density were opposite to that predicted to lead to a positive density–area relationship: log size and conspecifics had weak negative effects on growth rate (Table 3—Finite



**Fig. 1** Effects of patch size and number of conspecifics on the predicted proportion of logs visited by *Odontotaenius disjunctus* within 12 min of release (a) and with at least one immigrant after 1 week (b) [ $\pm$  standard error (SE)]. Plain bars Predicted proportions under the full model (WOOD + LG + CON, H5, Table 2). For comparison, cross-hatched bars show the predicted proportions if only resource availability (=surface area per beetle) is important (WOOD, H2, Table 2). For details on statistical models, see Table 2

**Table 3** Comparison of hypotheses estimating beetle response to patch size and conspecific abundance during settlement and reproduction

Hypotheses	<i>k</i>	$\Delta AICc$	$R^2$ (%) <sup>a</sup>	ww- <i>p</i> <sup>b</sup>	AUC <sup>c</sup>	<i>w</i> <sup>d</sup>
Probability that a beetle visited a log within 0.5 m of release						
<b>H4. WOOD + CON</b>	<b>4</b>	<b>0.00</b>	<b>17.8</b>	<b>0.08</b>	<b>0.73</b>	<b>0.52</b>
<b>H5. WOOD + LG + CON</b>	<b>5</b>	<b>0.20</b>	<b>19.8</b>	<b>0.44</b>	<b>0.73</b>	<b>0.47</b>
H1. Intercept only	1	9.62	0.0	0.58	0.50	0.00
H3. WOOD + LG	2	22.18	-13.1	0.55	0.53	0.00
H2. WOOD	1	22.59	-16.3	0.32	0.49	0.00
Full model: binomial logistic regression; $\sim -1.91 + \text{WOOD} + 0.63 \text{ LG} + 3.14 \text{ CON}$ (opp. sex) + 1.88 CON (one pair) + 2.67 CON (two pairs); <i>n</i> = 118; $\Sigma w^d$ : WOOD = 1.0, LG = 0.47, CON = 1.0						
Probability that a log contained at least one immigrant a week after it was colonized						
<b>H5. WOOD + LG + CON</b>	<b>5</b>	<b>0.00</b>	<b>44.2</b>	<b>0.31</b>	<b>0.85</b>	<b>1.00</b>
H3. WOOD + LG	2	13.70	27.0	0.20	0.77	0.00
H4. WOOD + CON	4	19.14	25.8	0.02	0.80	0.00
H1. Intercept only	1	37.42	0.0	0.80	0.50	0.00
H2. WOOD	1	38.92	-1.8	0.01	0.59	0.00
Full model: binomial logistic regression; $\sim -0.70 + \text{WOOD} + 2.46 \text{ LG} + 2.05 \text{ CON}$ (opp. sex) + 2.35 CON (one pair) + 2.10 CON (two pair); <i>n</i> = 117; one log lost to fire ant colony; $\Sigma w$ : WOOD = 1.0, LG = 1.0, CON = 1.0						
Probability that a log retained at least one of its original residents after being exposed for 1 week						
<b>H4. WOOD + CON</b>	<b>3</b>	<b>0.00</b>	<b>15.8</b>	<b>0.91</b>	<b>0.50</b>	<b>0.38</b>
<b>H1. Intercept only</b>	<b>1</b>	<b>1.25</b>	<b>0.0</b>	<b>0.19</b>	<b>0.47</b>	<b>0.20</b>
<b>H3. WOOD + LG</b>	<b>2</b>	<b>1.59</b>	<b>5.2</b>	<b>0.40</b>	<b>0.63</b>	<b>0.17</b>
H2. WOOD	1	2.13	-2.5	0.55	0.74	0.13
H4. WOOD + LG + CON	4	2.47	15.8	0.56	0.75	0.11
Full model: binomial logistic regression; $\sim -0.53 + \text{WOOD} + 0.08 \text{ LG} + 0.51 \text{ CON}$ (one pair) + 2.40 (two pair); <i>n</i> = 40; $\Sigma w$ : WOOD = 0.80, LG = 0.28, CON = 0.49						
Finite growth rate in a log after one reproductive season						
<b>H2. WOOD</b>	<b>2</b>	<b>0.00</b>	<b>55.4</b>			<b>0.68</b>
H3. WOOD + LG	3	2.30	56.0			0.21
H4. WOOD + CON	4	4.10	58.2			0.09
H5. WOOD + LG + CON	5	6.70	59.2			0.02
H1. Intercept only	2	16.74	0.0			0.00
Full model: linear regression; $\sim -3.68 + \text{WOOD} - 0.13 \text{ LG} - 0.23 \text{ CON}$ (two pairs) - 0.09 CON (three pairs); <i>n</i> = 27; 2 logs were lost to Hurricane Gustav; Response: $\ln(\text{number of beetles present in November}/\text{number of beetles present in June} + 0.5)$ ; $\Sigma w$ : WOOD = 1.0, LG = 0.23, CON = 0.11						

Hypotheses (H1–H5) are described in Table 2 together with coefficients (WOOD, LG, and CON),  $\Delta AICc$  and conspecific abundance levels in movement analyses and growth rate analyses

Bold values indicate highly informative models ( $\Delta AICc < 2$ )

<sup>a</sup>  $R^2$ , Nagelkerke’s pseudo- $R^2$  (explanatory value: 0 % = none, 100 % = perfect; Nagelkerke 1991)

<sup>b</sup> WW-*p*, *p* value from a Wald–Wolfowitz runs test (0.025–0.975 = residuals are independent)

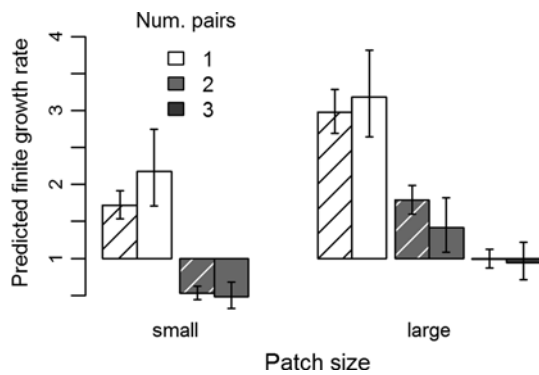
<sup>c</sup> AUC, Area under receiver operating characteristic curve (predictive value: 0.5 = random, 1.0 = perfect)

<sup>d</sup> *w*, Akaike weight (probability a model is the “true” one),  $\Sigma w$  is the summed Akaike weight (probability predictor is in the “true” model)

growth rate in a log after one reproductive season). Likewise, responses related to growth rate (fecundity, juvenile survival, adult survival, and juvenile body size) were only weakly influenced, if at all, by log size or conspecifics beyond that expected with the associated changes in resource availability per beetle (ESM Appendix A).

### Discussion

This study is one of only a few performed to date to experimentally compare multiple hypotheses underlying an observed density–area relationship. Previous studies of mechanisms underlying density–area relationships focused on movement-based processes (Table 1); our study



**Fig. 2** Predicted effects of patch size and number of conspecifics on *O. disjunctus* finite growth rate within a log after one reproductive season ( $\pm$ SE). *Plain bars* Combined effects of resource availability (surface area per potential pair), log size, and abundance of conspecifics. For comparison, *cross-hatched bars* show the effect of resource availability alone; log size and the number of beetle pairs are set to intercept values (small logs, one pair)

is unique in that it simultaneously compares the effects of patch-size and conspecifics on both movement and reproductive fitness. By doing so, we found support for the hypothesis that movement-based processes—rather than within-patch processes—are responsible for the positive density–area relationship observed for *O. disjunctus*. Conspecific attraction and large log attraction were evident when beetles immigrated, but we did not see a subsequent advantage to large logs and conspecifics during reproduction.

Conspecific attraction may be an underrated contributor to density–area relationships among animal populations. The authors of a meta-analysis of density–area relationships concluded that when a density–area relationship exists, it is more strongly positive for birds and insects than for other taxa (Connor et al. 2000). Response to conspecific cues among birds and insects of the same species are well-documented (Murlis et al. 1992; Valone 2007). Our study is the first to provide evidence that passalids can detect each other from outside a log. Although the method of long-distance passalid communication is unknown, insects in general frequently use pheromones (Murlis et al. 1992). The most similar insect to *O. disjunctus* for which long-distance communication has been studied is *Osmoderma eremita*, which, like *O. disjunctus*, is slow-moving, scarabaeoid, and saproxylic. Traps baited with male-produced pheromones of *O. eremita* strongly attracted females, but, interestingly, may have also attracted males (sample sizes were too small to be conclusive) (Larsson et al. 2003). Only two studies, one of a bird (least flycatcher; Fletcher 2009) and the other of an insect (Mexican bean beetle; Turchin 1987), have explicitly considered the potential for conspecific attraction to lead to a positive density–area relationship.

There are many reasons why conspecific attraction can increase fitness without affecting within-patch processes. Conspecific attraction may be selected for if it reduces costs during search or settlement (Stamps 2001). Search costs are reduced if individuals are able to find a habitat faster by following conspecific cues, while settlement costs are reduced if conspecifics decrease the time and energy required to settle. Bark beetles (Coleoptera: Curculionidae: Scolytinae) provide well-studied instances in which conspecific attraction reduces both search and settlement costs, but does not provide a benefit during reproduction (Kausrud et al. 2011). In general, a pioneer bark beetle emits aggregation pheromone to guide other beetles (reducing their search time) so that together they can overcome the tree's defenses (reducing settlement costs). As with *O. disjunctus*, conspecifics have a negative influence on bark beetle reproductive success (e.g. Robins and Reid 1997). Our data were not designed to provide evidence of reduced search time, but the fact that *O. disjunctus* could perceive conspecifics from outside the log suggests that this is a good possibility. As for settlement costs, *O. disjunctus* consumes only dead trees so it does not require conspecifics to overcome tree defenses. However, beetles reliant on dead wood face the challenge of assessing conditions left by previous beetle and fungal inhabitants, who can inhibit or facilitate their colonization (Weslien et al. 2011). For example, we have yet to find *O. disjunctus* in anything but logs decayed by white rot (as opposed to brown rot; both rots can be caused by various fungal species). Conspecifics could quickly convey or confirm information about the suitability of wood. On the other hand, it is probable that saproxylic beetles can directly detect volatiles emitted by fungi (Olsson et al. 2012), which would make natural selection for an indirect cue of quality (i.e. conspecifics) less likely (Stamps 2001). Thus, it is unclear whether conspecifics are used as an indirect cue of habitat quality.

Although conspecifics do not enhance reproductive success within a patch, proximity to conspecifics post-dispersal may be beneficial if conspecifics increase mating opportunities (Allee 1927) or reduce predation risk (Nelson and Jackson 2008). Once in the reproductive season, pairs of a related passalid species, *Heliscus tropicus* Percheron, will aggressively defend against conspecific intruders (Valenzuela-González 1986), and aggressive behaviors by mating pairs of *O. disjunctus* have also been documented (Schuster 1983; Wicknick and Miskelly 2009). Our data suggest, however, that pairs are easily disrupted during the establishment phase of settlement: only one of the original 40 resident pairs was still together at the end of our settlement experiment, and 33 new pairs had formed. This high mate turnover implies that the decision to investigate a log when conspecific pairs are present has the potential to yield both a mate and a territory. Even if a beetle is unable to take over a



territory, settlement near an occupied territory could provide extra-pair mating opportunities. A similar strategy seems to be used by the female black-capped chickadee which tends to select nest sites close to that of a neighbor if the neighboring male is more highly ranked than her partner (Ramsay et al. 1999). Extra-pair copulation is common for birds (Griffith et al. 2002) and has been documented for other socially monogamous scarabaeoid beetles (e.g. Emlen 1997). However, reduced predation risk cannot be ruled out. *O. disjunctus* emits a distinct call when disturbed, but whether this call warns neighbors of danger is unclear (Buchler et al. 1981; Schuster 1983). Furthermore, proximity to conspecifics may increase predation risk if larger predators (e.g. woodpeckers or bears) are attracted to high densities of insects.

Finally, beetles may not prefer to live with conspecifics so much as live where conspecifics have previously lived. This might occur if conspecifics hasten the decay of a log and make the log more accessible (i.e. more easily chewed) for successors. This idea is supported by the fact that although beetles were more likely to settle in logs originally occupied by conspecifics, many of the former residents left so that the total number of beetles was usually one pair. We expect that if our logs had been larger, beetles may have remained in logs together (but in separate territories), resulting in the higher local densities found in nature.

Beetle preferences did not correspond with post-settlement performance. This mismatch between habitat selection and reproductive success is not rare among insects, however. A review of phytophagous insect oviposition behavior concluded that although most insects preferentially select hosts that impart the highest offspring fitness, as many as 24 % of species do not (Mayhew 1997). Behaviors that do not correlate with fitness might occur if a trait is vestigial, if a species' traits are phylogenetically or physiologically constrained, or if a species has not had time to adapt to a newly colonized habitat (Mayhew 1997). Alternatively, habitat preference may increase lifetime fitness but not short-term fitness measured in most studies (including our own). For example, additional insulation provided by large logs (Lindberg et al. 2004) could improve *O. disjunctus* survival during the winter. Alternatively, the slower decay rate of large logs (Zell et al. 2009) could allow multiple generations to settle within their natal log instead of risking dispersal outside of a log to find new territories. High philopatry has been shown for a beetle similar to *O. disjunctus*, *O. eremita*, which lives in long-lasting tree hollows. In a radio-telemetry experiment, most adults (82–88 %) did not move from their original tree (Hedin et al. 2008).

The ability of movement-based processes to result in a positive density–area relationship indicates that movement is a significant process contributing to density within coarse woody debris for *O. disjunctus*. If movement among patches was rare at this scale, then we would expect

within-patch processes to dominate patterns of density. Östman et al. (2009) found that the relationship between patch size and density of multiple arthropod species was qualitatively different for isolated islands versus islands close to the mainland, supporting their hypothesis that the balance between movement-based and within-patch processes shifts depending on the isolation of a patch.

We would also expect movement-based processes to have a strong signal in patterns of density for species that must move and select new habitat often, such as those living in ephemeral habitats. For example, the positive density–area relationship for dung beetle density on ephemeral dung pads is strongly influenced by colonization patterns (Finn and Giller 2000). In coarse woody debris, early decay stages last only a short time (months as opposed to years in mid- and late-decay stages), so we expect species specialized on early decay states to show an even stronger influence of movement-based processes than *O. disjunctus*.

How well density indicates habitat quality has long been a question in ecology (Van Horne 1983). Although positive density–area relationships can result from increased quality in large patches for some species (e.g. Matter 1997), our results suggest that the higher density of *O. disjunctus* in large logs found in previous surveys is likely to be due to preference during settlement rather than increased patch quality. These results underscore the importance of testing the mechanisms that underlie models of distribution.

Understanding the mechanisms underlying population distributions may be particularly important for saproxylic beetle conservation. Up to 25 % of saproxylic beetle species are threatened or endangered (Dahlberg and Stokland 2004). There are clearly many species that rely specifically on large-diameter logs, and average diameter is one of the main attributes of coarse woody debris to be negatively affected under current forest management strategies (Gossner et al. 2013). We therefore caution against the conclusion that the special conservation importance of large-diameter logs is significantly diminished by our data. However, for those species for which the importance of large-diameter logs is inferred from a positive density–area relationship, the mechanisms underlying the positive density–area relationship need to be tested. As our data show, a positive density–area relationship may occur independently of habitat quality. For some species of conservation concern, it is possible that a greater quantity of medium-diameter wood (which is easier to acquire than veteran-tree sized wood) is an appropriate conservation intervention.

**Acknowledgments** We would like to thank Amanda K. Accamando, Forrest Dillemath, and Erick Reitschier for valuable field assistance. We are indebted to Louisiana State University for the use of its property. This work was supported by the Louisiana State University and National Science Foundation Grants DEB-0211359 and DEB-0515764 (and three REU Supplements) to J.T.C., a Louisiana State

University Board of Regents Fellowship, two Louisiana State University BioGrads Awards, two Sigma Xi Grants-in-Aid of Research, and the American Natural History Museum's Theodore Roosevelt Memorial Fund to H.B.J.

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