

Habitat-Specific Movement and Edge-Mediated Behavior of the Saproxylic Insect *Odontotaenius disjunctus* (Coleoptera: Passalidae)

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ABSTRACT The ability to disperse among patches is central to population dynamics in fragmented landscapes. Although saproxylic (=dead wood dependent) insects live in extremely fragmented forest ecosystems and comprise a significant proportion of the biodiversity therein, few studies have focused on dispersal of members in this group. We quantified the terrestrial movements of *Odontotaenius disjunctus* Illiger, a common saproxylic beetle in eastern North American forests. Movement behavior of individual beetles was measured in deciduous forest and two common matrix (=unsuitable) habitats (urban lawn and cattle pasture). Probability of emigrating from a forest fragment was assessed at the high-contrast boundary between forest and pasture. Seasonal, diurnal, and sex-biased patterns of *O. disjunctus* dispersal were determined from captures at drift fences encircling inhabited logs. Movement was 1.6 and 2.7 times faster and 1.1 and 1.5 times more linear in suitable habitat (forest) than in unsuitable matrix (lawn and pasture, respectively). Net displacement in the forest exceeded predictions of a correlated random walk, but net displacement in matrix habitats was less than expected. When confronted with a high-contrast boundary, *O. disjunctus* was 14 times more likely to move toward the forest than the pasture. The importance of temperature was indicated by its positive relationship with movement rate and increased diurnal and warm season dispersal activity. Reluctance to cross boundaries into open fields and slow movement within open fields suggest a low likelihood of terrestrial *O. disjunctus* movement among forest fragments.

KEY WORDS bess beetle, horned passalus, coarse woody debris, landscape matrix

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).

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 nonforest (matrix) habitats.

We analyzed the movement of the saproxylic beetle, *Odontotaenius 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 terres-

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trial movement (e.g., displacement, speed, and linearity) of *O. disjunctus* as it traveled within the forest and within nonforested 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), we 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.

We tested several predictions about how *O. disjunctus* moves. First was the prediction that *O. disjunctus* would move faster and more linearly in the forest than in nonforest 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).

We 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 (Kareiva 1982). Deviation from the net displacement predicted by a correlated random walk model can signal nonrandom 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). We expected that, as a forest specialist, *O. disjunctus* would avoid crossing into nonforested habitat when confronted with a high-contrast boundary.

Study System. *Odontotaenius 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* shows a preference for hardwood that has been dead for at least 2 yr, particularly oak (Gray 1946). A lifespan of at least 2 yr has been recorded in the wild (Gray 1946); however, other passalid species in captivity have survived for >4 yr (Schuster and Schuster 1985). *Odontotaenius floridanus*, whose range is restricted to peninsular Florida, and *O. disjunctus* are the only pas-

salid species in eastern North America (Schuster 1994), although between 700 and 1,000 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 mo), 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 its walking behavior. During >100 h of direct observation of passalid beetles, we did not observe any flight. Furthermore, flight intercept traps deployed in the forest for 6 mo (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 4-mo 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. *Odontotaenius disjunctus* adults were tracked after their release within forested habitat and open fields (urban lawn and cattle pasture) to determine whether movement behavior differed among habitat types. Using a hatchet to carefully dissect galleries, we 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 <2

d before 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 or 1900–2000 hours CDST). Grass culms averaged 7.9 ± 0.3 (SE) cm ($n = 19$ 1-dm² quadrats) in height, with a density of 3.2 ± 0.2 culms/dm². 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; $t_{47} = -2.76$, $P = 0.008$) and culm densities that were no different (4.1 ± 0.3 culms/dm²; $t_{47} = 1.49$, $P = 0.143$) than in the pasture. Release points in the forest or open fields were >30 m from the edge.

Odontotaelius disjunctus beetles were released one at a time by laying their collection cups on the ground and allowing them to leave on their own. Surveyor flags were used to mark the location of each beetle at 1-min intervals (Turchin et al. 1991, Cronin et al. 2001). Beetle dispersal did not seem 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 >5 min or after 30 min had elapsed. During preliminary observations we found beetles that stopped movement for 5 min were unlikely to move within the next 2 h. Using a triangulation program written in R 2.7.2 (available on 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, $n = 66$).

We 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 dis-

placement 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. We included air temperature and relative humidity as covariates in our 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 (2002). Akaike's information criterion for small sample sizes (AIC_c) was used to select the best model or the best set of models. The model with the smallest AIC_c value was considered the best model. Models with $AIC_c \leq 7$ points greater than the lowest AIC_c 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), we assessed whether sex or size predicted movement. The model selection process was identical to that described above.

We 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 $<99\%$ or $>99\%$ of the simulated tracks (increased from 95% to adjust for inflated type I error rates associated with multiple tests) is scored as a rejection (i.e., not fitting a correlated random walk). 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), whereas ordered logistic regression allows for an ordered multilevel 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 we 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 (10 individuals in the morning and 10 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 min of movement. Dividing the possible directions into thirds, each beetle's path was assigned to one of three categories (toward the forest, on the boundary, and toward 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 mo (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 hours CDST) from 1 to 23 June 2005. Because of a slowdown in dispersal activity at the end of June, twice daily trap-checks were discontinued until September and then from 12 to 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 8–10 wk after 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 daylength, and time since the beginning of the experiment. Daylength 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 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 exact test for each fenced log.

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

All analyses were conducted in R version 2.7.2 (R Development Core Team 2008). All reported intervals are 95% confidence intervals (CIs).

Results

Habitat-Specific Movement Behavior. Displacement rate, velocity, and linearity were greater in the forest than in open fields (forest > lawn > pasture; Fig. 1). Habitat, a highly informative predictor of movement behavior, was present in the best set of models for all three sample sets (Table 1). The best model predicting movement behavior included habitat, capture method, temperature, and relative humidity (Table 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; Fig. 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; Fig. 1).

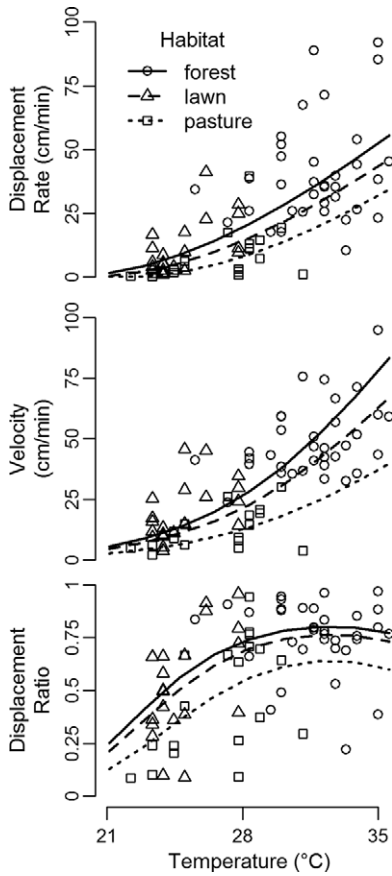


Fig. 1. Relationship between movement behavior (displacement rate, velocity, and net-to-gross displacement ratio) and temperature (the most important weather variable; Table 1). Open symbols indicate raw data in the forest (circles), lawn (triangles), and pasture (squares). Lines and closed symbols represent expected values at average relative humidity (63%).

The fastest beetles were those that had been collected in pitfall traps before 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 (Tables 1 and 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 1), and temperature and habitat explained 4–5 times more model variance (Table 3). Temperature and relative humidity were both positively related to movement rate and linearity (Table 2), although relative humidity explained only one fourth the model variance of either temperature or habitat (Table 3). Temperature and habitat tended to explain equivalent proportions of the variation in movement variables (Table 3). The best models for predicting displacement rate and velocity had r^2 values that exceeded 70% (Table 3), but the best models predicting displacement ratio had r^2 values <40%.

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 three times more important when predicting path linearity (Table 3). Sex was of negligible importance when predicting displacement rate and velocity (Table 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 1), but the model including length may have had some information value ($\Delta AIC_c = 2.96$; a model with $2 < \Delta AIC_c$

Table 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

Response	Sample size	Model	K	ΔAIC_c	w_i
(1) Movement behavior	(a) ($n = 76$)	Habitat + capture method + T + T ² + RH	8	0.00	0.68
		Habitat + T + T ² + RH	7	1.53	0.32
	(b) ($n = 58$)	Habitat + sex + T + T ² + RH	8	0.00	0.99
		Habitat + T + T ² + RH	6	0.00	0.74
	(c) ($n = 28$)	Habitat + length + T + T ² + RH + length	7	2.96	0.17
		T + T ² + RH	5	4.53	0.08
(2) Correlated random walk	$(n = 76)$	Habitat	4	0.00	0.61
		Habitat + RH	5	2.28	0.19
		Habitat + T + T ²	6	4.41	0.07
		T + T ²	4	4.46	0.07
		T + T ² + RH	5	6.68	0.02
		Habitat + T + T ² + RH	7	6.83	0.02
		t + T + T ² + DL + DL ²	6	0	0.59
(3) Dispersal activity	$(n = 72)$	t + T + T ² + DL + DL ² + RH	7	0.76	0.41

Only those models for which ΔAIC_c was <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. (a) models based on full dataset; (b) models based on subset of data for which sex information was available; (c) models based on subset of data for which body size measurements were available. See Materials and Methods for details.

K , the no. of estimated model parameters; ΔAIC_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.

Table 2. Movement behavior in response to habitat type and capture method and change in weather conditions

Independent variables	Displacement rate (cm/min)			Velocity (cm/min)			Net-to-gross displacement ratio		
	Average	95% CI		Average	95% CI		Average	95% CI	
		Lower	Upper		Lower	Upper		Lower	Upper
(1) Response to habitat and capture method									
Log-captured									
Forest	20.84	13.01	30.50	28.21	20.04	39.70	0.74	0.55	0.87
Lawn	15.31	6.73	27.36	22.68	14.17	36.31	0.70	0.42	0.88
Pasture	8.84	3.21	17.25	13.40	8.79	20.41	0.56	0.31	0.78
Pitfall trap-captured									
Forest	36.28	24.40	50.51	42.37	28.78	62.38	0.81	0.62	0.92
(2) Impact of a 1-U increase in weather conditions									
T (°C)	0.19	0.07	0.36	1.21	1.14	1.28	1.17	1.01	1.36
T ² (°C ²)	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% RH).

(2) The average change in each movement behavior associated with a 1-U 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.

< 7 has some information value according to Burnham and Anderson, 2004).

Correlated Random Walk. 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 1). Fifty-one percent of beetles moving in the forest displaced further than expected by a correlated random walk model (Fig. 2). In contrast, beetles in lawn and pasture tended to displace 83 and 78% less than expected, respectively (Fig. 2).

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, whereas only 5% (CI = 0–25%) moved toward 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 to -2%/°C²) and intermediate daylength (CI = 22–51%/MJ/m²; quadratic CI = -0.001–0.002%/MJ²/m⁴) and decreased with time since the observations began (CI = -2–4%/wk; McFadden’s $\rho = 56.6\%$; Tables 1–3; Fig. 3). The second best model explaining weekly dispersal activity included relative humidity (Tables 1–3) and indicated a slightly negative correlation between relative humidity and odds of dispersal (-4.1 to +0.02%/humidity).

Overall, incompletely sclerotized beetles comprised $28 \pm 5\%$ SE of dispersers. Fifty-nine percent ($\pm 6\%$) of dispersers were female, a percentage not significantly different from the sex ratio within nearby

Table 3. Proportion of variance explained by each independent variable in the two best models predicting movement behavior (see Table 1)

Sample set	Independent variables	Displacement rate	Velocity	Net-to-gross displacement ratio
(1) Best model: habitat + capture method + T + T² + RH (n = 76)				
T ^a		28.6%	31.6%	15.6%
Habitat		28.0%	31.4%	12.7%
Capture method		6.7%	4.6%	2.7%
RH		6.7%	7.2%	3.1%
Total percent variance explained (r ²)		70.0%	74.8%	34.1%
(2) Best model: habitat + sex + T + T² + RH (n = 58)				
T ^a		32.3%	33.8%	15.4%
Habitat		31.3%	35.3%	15.5%
Sex		0.3%	0.2%	4.3%
RH		6.6%	6.8%	2.8%
Total percent variance explained (r ²)		70.5%	76.1%	37.9%

Relative importance is measured as the average proportion of variance explained by each variable (*sensu* Lindemann et al. 1980). Relative importance for each independent variable sums to the total variance explained (r²).

^a 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.

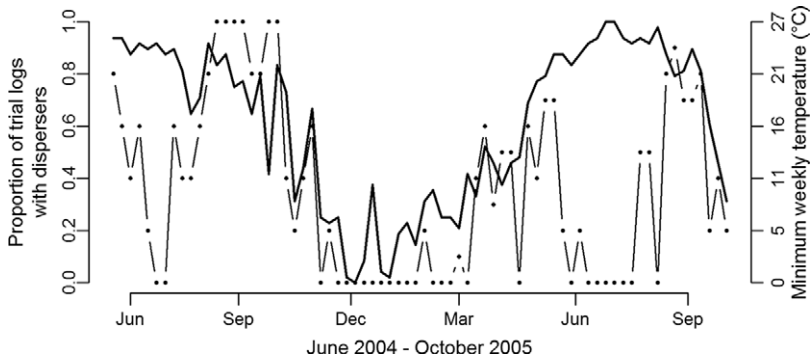


Fig. 2. Probability that a beetle’s net squared displacement is lower, equal to, or greater than the predictions of an empirically based, beetle-specific correlated random walk (see Materials and Methods for description). Error bars are 95% confidence intervals.

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 ($P < 0.001$).

Odontotaenius 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; also see Introduction) and empirical findings for a *Prokelisia* planthopper (Haynes and Cronin 2006), a flightless tansy leaf beetle (Chapman et al. 2007), and the bog fritillary butterfly (Schtickzelle et al. 2007). Slower movements in an 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 scan 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 that 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. However, faster movement in matrix may be optimal but animals may be unable to maintain optimal movement because of 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. 2008). 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 (Conradt et al. 2000, Jonsen and Taylor 2000, Cronin 2003, 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

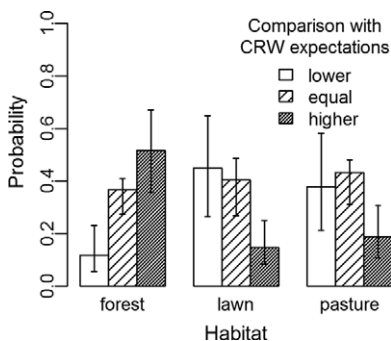


Fig. 3. Patterns of dispersal activity of *O. disjunctus* by week. Dispersal data represent the proportion of trial logs (2004, $n = 5$; 2005, $n = 10$) from which one or more beetles were caught each week.

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 >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 with other resources used by insects, decaying wood is relatively stable; coarse woody debris in Louisiana bottomland hardwood forests exhibit a half-life of 9–14 yr 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 >100 yr 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 (Ranius and Hedin 2001). Assessments of saproxylic insect diversity should therefore include methods designed to capture nonflying insects (e.g., ecollector or pitfall traps; Ranius and Jansson 2002, Alinvi et al. 2007) in addition to more traditional methods targeting flying insects.

Our data suggest that nondispersing 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 nondispersing 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 our system) or such individuals are difficult to distinguish from those engaged in routine movements. Even so, the movement of naturally dispersing beetles in our experiment was comparable to that of experimental beetles in shape if not in scale: capture method was not an important predictor of linearity. We expect the data collected from nondispersing 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 Ekblom 1994), it was inadequate for more than one half of the individuals observed in this study. This predic-

tion failure was caused in part by 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) suggested that autocorrelation can result when steps are measured on a scale smaller than is meaningful to the organism. However, we 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 toward 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. However, 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 (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 study 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 long-horned beetle; 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 review). 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 show equal dispersal tendencies, especially when responsibility

for resource defense is shared by both partners (Greenwood 1980, Greenwood and Harvey 1982; see also Schuster 1983 and Schuster and Schuster 1985). 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.

In summary, 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. Our results also support the growing body of literature (Ranius and Hedin 2001, Starzomski and Bondrup-Nielsen 2002, Jonsell et al. 2003) that shows 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, despite these challenges. For example, *O. disjunctus* was found in each of 24 forest patches surveyed in the Mississippi alluvial floodplain of Louisiana—an area distinctive in Louisiana for its particularly high forest fragmentation because of agriculture (H.B.J., unpublished data). Two nonmutually 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 show 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, we 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, we 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.

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