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Explaining movement decisions of forest rodents in fragmented landscapes

Carol E. Rizkalla*, Robert K. Swihart

Department of Forestry and Natural Resources, Purdue University, West Lafayette, IN 47907, USA

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ABSTRACT

Functional connectivity is a measure of the interaction of landscape structure and a species' dispersal ability to determine the degree to which a landscape facilitates movement among patches. Dispersal through an inhospitable matrix requires that a species is willing to enter the matrix and can successfully colonize another habitat patch. Many connectivity indices have been developed which incorporate various attributes of the landscape, but little empirical evidence of the accuracy of these indices is available. We studied the ability of white-footed mice (*Peromyscus leucopus*), eastern chipmunks (*Tamias striatus*), and southern flying squirrels (*Glaucomys volans*) to move through agricultural fields in west-central Indiana. Radio-collared animals were translocated into corridors that either were connected to or unconnected from an associated forest patch to determine their willingness to enter the matrix. Animals also were translocated into fields to determine how motivation to find resources influences movement through the matrix. All species demonstrated a strong motivation to find the forest. Animals were capable of moving through the matrix successfully, however, we were unable to determine whether they would do so willingly. Initial bearing was an important predictor for successfully reaching a forest patch, which has implications for modeling dispersal. Additionally, abiotic variables, such as temperature and precipitation, had a strong effect on latency to move from the release site. Although weather often correlates with seasonal migration, our study emphasizes the importance of weather in influencing short-term decisions on timing of movement.

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1. Introduction

Recognition that a heterogeneous matrix can affect animal movement has increasingly called for empirical estimation of matrix resistance or permeability for various species (e.g. Bélisle and St. Clair, 2001; Mazerolle and Desrochers, 2005; Pither and Taylor, 1998; Ricketts, 2001; Stevens et al., 2004). Such estimates allow for the determination of effective distance between habitat patches, or functional connectivity. Functional connectivity can be decomposed into two components: the likelihood of an animal leaving a habitat patch to

enter the matrix; and, once in the matrix, the likelihood of successfully reaching a new patch (Ewers and Didham, 2006).

To assess functional connectivity for forest rodents in an Indiana landscape dominated by an agricultural matrix, we undertook experimental translocations of white-footed mice (*Peromyscus leucopus*), eastern chipmunks (*Tamias striatus*) and southern flying squirrels (*Glaucomys volans*). Mice and chipmunks are widespread in this landscape and may be insensitive to fragmentation (Moore and Swihart, 2005). Chipmunks, however, are slightly more closely tied to wooded habitat than are white-footed mice (reviewed by Nupp and

Swihart, 2000). Both species reach greater densities in small, isolated patches than in contiguous forest (Nupp and Swihart, 2000). Bowman et al. (2002) suggest that immigration behavior could lead to a negative density-area relationship, and homing experiments of both species have shown they are capable of crossing the matrix (Bender and Fahrig, 2005; Bowman and Fahrig, 2002). Of course homing behavior may be fundamentally different than dispersing through a landscape mosaic (Castellón and Sieving, 2006) and thus may not accurately estimate functional connectivity. Flying squirrels are found only in large patches, and they reach greater densities in less isolated patches (Moore and Swihart, 2005; Nupp and Swihart, 2000). The Siberian flying squirrel (*Pteromys volans*) only crosses fields when trees or bushes are present (Selonen and Hanski, 2003). Based on these findings, we hypothesized that southern flying squirrels view the matrix as hostile, due primarily to their glissant form of locomotion. They likely would be inefficient at crossing large treeless areas. Thus, in terms of ability to move through an agricultural landscape, we predicted the following species ranking: white-footed mouse ⩾ eastern chipmunk > southern flying squirrel.

Successful movement through the matrix may be influenced by a number of factors including, but not limited to: the distance to be traversed; the composition of the matrix; the motivation to find resources or conspecifics (Lima and Zollner, 1996); the tradeoff that crop cover likely causes between perceptual range and predation risk (Zollner and Lima, 2005); and the size or attractiveness of a forest patch (Matter et al., 2005). Larger patches may be more likely to be intercepted by an animal (Gutzwiller and Anderson, 1992) and also would have a larger horizon for an animal to perceive (Olden et al., 2004). Such factors have been incorporated into dispersal rules within spatially explicit population models that include connectivity (e.g. Brooker et al., 1999; Goodwin and Fahrig, 2002). We incorporated these variables in the development of what we term "connectivity" models.

Other factors that have not been incorporated into movement rules also may affect an individual's dispersal success. Zollner and Lima (1999a) demonstrated that moonlight increases habitat detection in mice, although moonlight also could increase the ability of predators to detect prey. Additionally, cloud cover can obscure moonlight. Once the translocations had begun, we observed that some animals that had yet to move towards a forest patch were found in the forest after a day or night of heavy rain. Therefore, we assembled temperature and precipitation data for past translocations and continued to collect weather data for the duration of the study. The initial bearing of animals also may affect an individual's likelihood of reaching the target patch (Gutzwiller and Anderson, 1992). We considered bearing as a crude estimation of search strategy. Thus, weather, moonlight and bearing variables were incorporated into separate analyses designated as "full" models. Here, we show that weather and search strategies are important variables to consider in explaining movement through the matrix and may influence estimates of functional connectivity. Although it is unlikely that future connectivity and dispersal models will account for such daily variation, it is important to recognize that this variation exists, as long periods of unfavorable weather may affect dispersal.

2. Methods

To determine movement ability through the matrix, we conducted experimental translocations of radio-collared animals in the Indian Pine Study Area in west-central Indiana (for further description, see Sheperd and Swihart (1995)). This 812 km² area consists of approximately 10% forest cover and is dominated by an agricultural matrix, primarily corn and soybeans (70%). We selected treelines and grassy fencerows (hereafter, corridors) which were connected to forest patches, such that an animal would not have to enter the matrix to reach the forest. Corridors unconnected from a forest patch also were selected, such that an animal had to cross the matrix to reach the forest. Additionally, animals were released directly in corn or soybean fields.

From May–September 2003–2006, mice, chipmunks, and flying squirrels were captured in Sherman traps baited with black oil sunflower seed. Study animals were held in cages at an animal care facility for up to 3 days prior to collar attachment and translocation, maintained at a constant temperature and a 12L:12D photoperiod. Animals were provided rodent chow, sunflower seed, and water ad libitum. All cages contained pine shavings. Additionally, chipmunks were provided with a Sherman trap locked open, and flying squirrels were provided with a nest box.

Because we suspected that juveniles would be at a greater risk of predation, we only used adults in translocations. Furthermore, pregnant or lactating females were not used. Juveniles in search of breeding territory may have more motivation to disperse; however, the adults were placed in a novel landscape which likely forced movement and provided a representation of natural dispersal (Bosschieter and Goedhart, 2005). Mice (>18 g), flying squirrels (>54 g) and chipmunks (>85 g) were fitted with 1.1, 1.6, and 2.0 g radio collars (Holohil Systems Ltd., Ontario, Canada), respectively. Animals were translocated into one of three release types (connected corridors, unconnected corridors or fields) at least 5 km from their capture site to ensure that they were not familiar with the area. Mice and chipmunks were transported in Sherman traps and flying squirrels in nest boxes. Chipmunks were released in the morning on clear days. Mice and flying squirrels were released at dusk on clear nights. Only one animal of a species was released into a corridor or field at a time.

Goheen et al. (2003) performed translocations with tree squirrels (*Sciurus* and *Tamiasciurus* spp.) in both pre-harvest and fallow seasons. Due to the seasonal limitations of chipmunk hibernation, we could not conduct many releases in fallow fields. Hence, we categorized translocation seasons into low crop height (bare field – 0.6 m) and full crop height (0.6–2 m). In each season, we began by performing releases 50 m from the forest in each release type. We refer to the forest defined by the release distance as the target patch. Other, "non-target" patches were at least 1 km from the release site. Although we arbitrarily defined the target patch as the one which was closest to the release site, we expected that individuals would choose the shortest distance and move to the closest patch (Bosschieter and Goedhart, 2005). Radio telemetry was used to locate chipmunks every evening and mice and flying squirrels every morning. Initially, two

animals of each species were tested at each distance. If at least one of the two individuals was successful in reaching the target patch within 7 days, we increased the distance of the subsequent release by 100-m. Seven days was chosen to maintain consistency with Goheen et al. (2003). To expedite determination of maximal movement distances, in the 2005–2006 seasons, rather than releasing two animals, we increased distances if the first individual was successful. We stopped incremental releases when three animals failed to reach the target forest from a particular distance. A failure was defined as an animal staying in the corridor or matrix, reaching a non-target patch, or suffering predation. Predation events were confirmed by finding a radio collar that had been chewed. Once an animal reached a forest patch or 7 days had elapsed since its release, it was recaptured, its collar removed, and the individual was returned to its capture site. Two animals, a mouse and a chipmunk, were released but could not be located and were excluded from analysis.

2.1. Statistical methods

We analyzed movement ability by recording three responses. First, we measured latency to move from the corridor or field. Latency served as our surrogate of willingness to move. Of those animals that moved, we modeled successful movement to a target or non-target forest patch. And for all animals, we considered a multinomial measure of success or failure (hereafter, fate):

1. failed to leave the corridor or field;
2. left the corridor or field, but did not reach a forest patch;
3. reached a non-target forest patch;
4. reached the target forest patch.

Thus, we considered two definitions of success. In the simpler binomial case, success was considered as movement through a corridor or the matrix to reach any patch. If an animal moved towards a non-target patch, they moved a much greater distance than had they reached a target patch. In the fate models (and in the translocations), the degree of success was divided into the multinomial categories listed above. The multinomial fate model constrained the definition according to the assumption that truly successful movement was dependent upon perception of the target patch.

We modeled these three response variables as a function of a set of landscape, weather, and behavioral variables. For the latency model, predictor variables included species, sex, the release type, release distance, area of the target forest patch, crop type, crop height, and a series of weather variables averaged over the days or nights before movement from the corridor or field. These included average temperature and rain, dominant cloud cover (Indiana State Climate Office, http://agmetx.agry.purdue.edu/sc.hly-geog.html) and average moonlight (US Naval Observatory, http://aa.usno.navy.mil/data/docs/RS_OneDay.html). We used the daily high temperature for chipmunks and the nightly low temperature for mice and flying squirrels. Cloud cover was categorized as clear (0%), few (<25%), scattered (25–50%), broken (50–90%), and overcast (>90%).

These variables also were used as predictors in the binomial and multinomial models of success, with the exception that the weather variables were averaged over the days or nights preceding arrival to a forest patch. If animals did not reach the forest, the data were averaged over the full 7 days, or the days preceding predation. We also included an additional predictor, initial bearing. Bearing was measured between 0° and 180° based on the first location of each animal approximately 12 h after release. A bearing of 0° indicated the animal moved towards the target patch. A bearing of 180° indicated movement in the opposite direction of the target patch. Eleven animals moved less than 5 m in the first 12 h. In these cases, bearing was estimated relative to the exit of the trap or nestbox. Overall, mean distances moved in the first 12 h for mice, chipmunks and flying squirrels, respectively, were 119.8 ± 25.7 m, 178.6 ± 31.4 m, and 336.8 ± 64.5 m. Therefore, bearing was easy to measure. In a few instances, chipmunks left the release site before the observer, and we were able to see the chipmunk move immediately and directly towards the target patch. Bearing and distance were not correlated ($r = 0.02$, $p = 0.78$).

To evaluate structural landscape connectivity (as traditionally considered from a static landscape map) for each species, we also constructed models with only landscape and species variables. These connectivity models did not contain any of the weather data or initial bearing of each animal. In both the full models (with weather variables) and the connectivity models, we also analyzed each species separately.

We classified vegetation structure in each corridor as grassy, shrubby, or treed. However, most of the unconnected corridors to which we had access were grassy. Thus, vegetation and release type were highly correlated ($r = 0.79$, $p < 0.001$). Therefore, we excluded vegetative structure from the analyses.

To analyze latency and success, we used Classification and Regression Trees (CART). CART models are a non-parametric alternative to regression models which recursively partition the dataset into increasingly homogenous groups with respect to the response variable (Breiman et al., 1984; Vayssières et al., 2000). They are especially useful for demonstrating nonlinear relationships (De'Ath and Fabricius, 2000). The tree is structured hierarchically, with the undivided dataset at the top (root node), followed by binary splits of the predictor variables (branches), ending at the terminal nodes (leaves) with the response. Continuous predictor variables are rank-transformed prior to iterative partitioning of the data (Urban, 2002). The proportion of variance explained by each predictor variable is represented by the branch length. The size of the tree is measured by the number of terminal nodes. Cross-validation and a cost-complexity index were used to determine the optimally sized tree (Vayssières et al., 2000). The cost-complexity index measures the additional accuracy of a tree given an increase in the number of nodes or a different variable at a node, and is thus, similar to Aikaike's Information Criterion (Akaike, 1973). A single tree was fit for each species and response variable using the RPART library (Therneau and Atkinson, 1997) in R 2.1.1. Regression trees, used to model latency, were evaluated with R^2. Classification trees, used to model success and fate, were evaluated with a misclassification rate. The success models were further assessed using

Receiver Operating Characteristic (ROC) curves (Fielding and Bell, 1997). The area under the curve (AUC) provides a measure of accuracy, where 0.5 indicates no difference between classification of true- and false-positives, and 1.0 indicates a perfect fit to the data. Generally, AUC > 0.7 is considered acceptable classification accuracy.

We tested for a difference in predation rates in corridors and fields by calculating Kaplan–Meier survival times in SPSS 14.0. For each individual, we calculated the number of days spent in corridors and/or fields and if predated, where it occurred. Suspected predation (where there were no chew marks on the collar) and mortality due to unknown causes were also included. The mean survival times for fields and corridors were compared with a χ^2 test in program CONTRAST.

3. Results

3.1. Translocations

We released a total of 52 mice, 64 chipmunks, and 38 flying squirrels (Table 1). Four animals were released at intermediate distances and included in the analyses but are not shown in Table 1. All three species moved towards the target patch from greater distances when released in unconnected corridors than connected corridors. Mice demonstrated lower mobility from fields, primarily due to failure to leave the field, rather than increased predation. Conversely, chipmunks and flying squirrels were successful in reaching the target patch from 1 km under high crops. Due to time constraints imposed by crop harvest and the spatial arrangement of patches in the study landscape, it was not possible to conduct translocations from greater distances to determine the threshold for successful movement. Confirmed predation rates based on telemetry days in a corridor or field, respectively, for mice were 2/93 and 4/106, for chipmunks, 4/77 and 2/83, and for flying squirrels, 1/57 and 0/24. Kaplan–Meier survival estimates showed no difference in mortality between the matrix and corridors ($X_1^2 = 0.4372$, $p = 0.51$).

3.2. Full models

The regression tree for latency explained 63.2% of the variance. All species moved more quickly from unconnected corridors and fields than connected corridors (Fig. 1). Additionally, movement from unconnected corridors and fields occurred sooner under clear and cloudy skies, rather than few clouds (<25% cover). In connected releases, when the target patch was greater than 3 ha, movement occurred sooner when there was little to no rain (<0.01 cm) and the temperature was warm (>15 °C). Latency to move from the corridor increased to 2 days or nights when there was more rain (>0.22 cm). Latency increased under intermediate levels of precipitation, with a further interaction with crop height. Latency was also high, or the animals did not leave the corridor, when the target patch was less than 3 ha. Recall that continuous variables are rank-transformed. Thus, measures such as 0.22 cm and 3 ha represent the median value defining a branch split, and not a true threshold.

The classification tree for successful movement toward a target or non-target forest patch (binomial definition) demon-

Table 1 – Summary of the fraction of individuals successfully reaching a target forest patch from a given distance in either connected or unconnected corridors or fields

Distance (m)	Species	Connected	Unconnected	Field
50	Mouse	3/4	2/4	2/4
	Chipmunk	4/4	4/4	3/3
	Flying squirrel	3/3	4/4	2/2
150	Mouse	2/4	2/4	2/3
	Chipmunk	2/4	3/4	3/4
	Flying squirrel	2/3	2/2	2/2
250	Mouse	0/6	2/3	1/4
	Chipmunk	1/5	2/4	2/2
	Flying squirrel	1/4	2/2	1/2
350	Mouse		2/2	0/3
	Chipmunk	1/2	1/4	3/3
	Flying squirrel		1/1	1/1
450	Mouse		0/3	
	Chipmunk	0/3	1/1	2/2
	Flying squirrel	1/1		
550	Mouse		0/3	
	Chipmunk		1/1	2/2
	Flying squirrel	0/3	1/1	0/1
650	Mouse			
	Chipmunk		1/1	1/5
	Flying squirrel		1/1	1/1
750	Mouse			
	Chipmunk		1/1	1/1
	Flying squirrel			
850	Mouse			
	Chipmunk		1/1	1/1
	Flying squirrel		1/1	1/1
1000	Mouse			
	Chipmunk			1/1
	Flying squirrel			1/1

strated reasonable accuracy with a 15% misclassification rate and AUC = 0.827. The single most important variable was bearing (Fig. 2). Animals with an initial bearing of less than 10° tended to successfully reach a patch. With a greater bearing, flying squirrels were successful. Mice and chipmunks that started out with a bearing greater than 10° were successful only under tall crops.

The classification tree for the multinomial definition of success (Fig. 3) showed the same structure as the tree for the binomial definition. All three species with an initial bearing tended to reach the target patch. Flying squirrels with a bearing greater than 10° reached a non-target patch. Additionally, under low crop height, mice and chipmunks often left the release site but failed to reach a forest patch. The misclassification rate was relatively high (27.9%).

The trees for the species-specific models are not shown. Mice demonstrated the same latency-weather relationship as in the full model ($R^2 = 0.733$). Movement occurred sooner under little rain (<0.04 cm) and warmer nights (>13.7 °C) or when there was more rain (>0.22 cm). Latency increased under intermediate levels of rain, and another interaction with
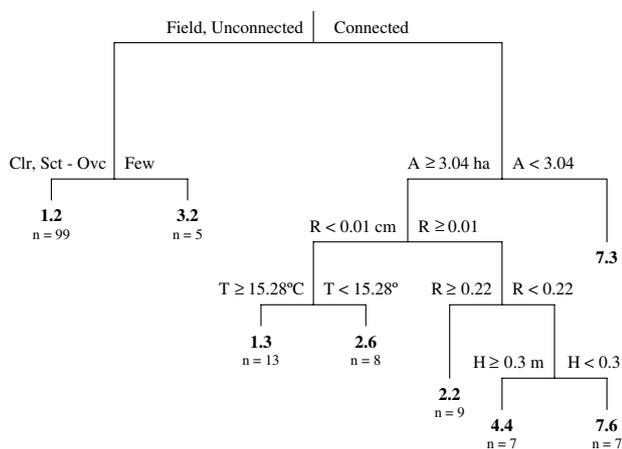
Fig. 1 – Regression tree for latency to move from the corridor or field. Predictor variables and the level defining a split are labeled at each branch split. Branch lengths are proportional to the amount of variance explained by the variable at the split. Terminal nodes represent latency. The sample size is provided below each node. $R^2 = 0.63$. Abbreviations: Clr, no cloud cover; Sct-Ovc, 25–100% cloud cover; Few, 1–25% cloud cover; A, area of target patch; R, rain; T, temperature; H, crop height.
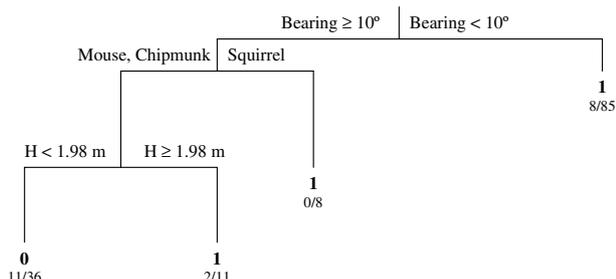
Fig. 2 – Classification tree for successful movement to a target or non-target forest patch. Terminal nodes with a bold-face 1 represent success. The misclassification rate is provided below each node. Overall misclassification rate = 0.15. AUC = 0.83. Abbreviations: H, crop height.
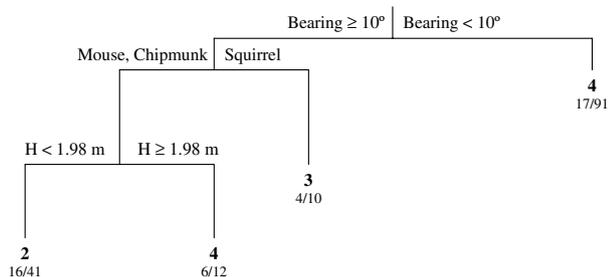

Fig. 3 – Classification tree for fate. Terminal nodes represent multinomial measure of success: 2, left corridor or field but did not reach forest; 3, reached non-target patch; 4, reached target patch. The misclassification rate is provided below each node. Overall misclassification rate = 0.28. Abbreviations: H = crop height.

temperature showed that mice did not leave the release site when it also was cold (<14.7 °C). Mice were not successful in reaching a patch when the matrix consisted of soybean fields, but they were successful from corn fields under lower moonlight (<63% visible disk) (misclassification rate = 37.5% and AUC = 0.81). Bearing was the most important variable to determine fate. With a bearing less than 10°, mice reached the target patch from distances less than 212 m, otherwise, they did not reach any patch. With a greater bearing, mice did not reach a patch in soybean fields, or in corn fields when the temperature was cool (<12.75 °C). In corn fields, with warmer temperatures, when crop height was <1.98 m, mice stayed at the release site. When crops were taller, they reached a non-target patch. This model had a 25% misclassification rate.

Chipmunks moved sooner from fields and unconnected corridors. Furthermore, larger animals (>89 g) moved on average a day earlier. From connected corridors, movement was more immediate when there was little rain (<0.05 cm). When there was more rain, latency was lower with warmer temperatures (>28.5 °C) ($R^2 = 0.415$). The cost-complexity index indicated that neither the classification tree for success or fate was reliable.

Movement latency of flying squirrels was less rapid when the target patch was small (<3.7 ha). When the target patch was larger, flying squirrels moved immediately from fields and unconnected corridors. In connected corridors, movement occurred sooner on warmer nights (>15.3 °C) ($R^2 = 0.567$). Because all flying squirrels that moved from the release site reached a target or non-target patch (i.e. they were all successful), we could not develop a model for success. The classification tree for fate simply showed that when the bearing was less than 40°, flying squirrels reached the target patch. Flying squirrels that moved on a greater bearing reached a non-target patch (misclassification rate = 15.8%).

3.3. Connectivity models

Removing weather variables and initial bearing reduced the variance explained by the latency model to 49.3%. The most important variable was still the release type, with more immediate movement from fields and unconnected corridors (Fig. 4). From connected corridors, movement occurred sooner when the target patch was large (>3 ha). Furthermore, chipmunks and flying squirrels moved sooner from distances less than 125 m. Between 125 and 300 m, latency was longer when the matrix was soybean, rather than corn. And latency increased to 4 days or nights from distances greater than 300 m. Mice moved on average 3 nights earlier when the target patch was very large (>8 ha) than with intermediate patch sizes. Latency for all species increased when the target patch was small.

The classification tree for the binomial model of success was more accurate than the full model (misclassification rate = 11.4% and AUC = 0.91) (Fig. 5). Mice were successful when the matrix was corn. When the matrix was soybean, mice were successful from distances less than 300 m and when the target patch was less than 6.3 ha. Flying squirrels were always successful. Chipmunks were successful when crop height was greater than 0.11 m. Under lower crop height,
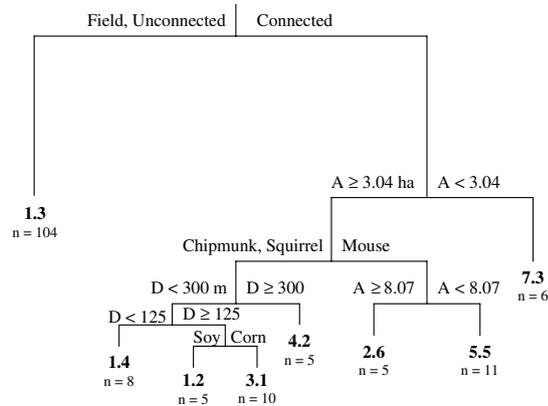
Fig. 4 – Regression tree for latency to move from the corridor or field with weather variables and bearing excluded from the model. The sample size is provided below each node. $R^2 = 0.49$. Abbreviations: A, area of target patch; D, release distance.

Fig. 5 – Classification tree for successful movement to a target or non-target forest patch with weather variables and bearing excluded from the model. The misclassification rate is provided below each node. Terminal nodes represent success (1) or failure (0). Overall misclassification rate = 0.11. AUC = 0.91. Abbreviations: A, area of target patch; D, release distance; H, crop height.
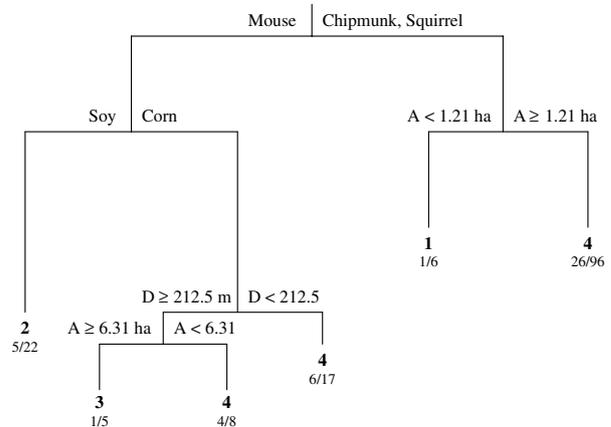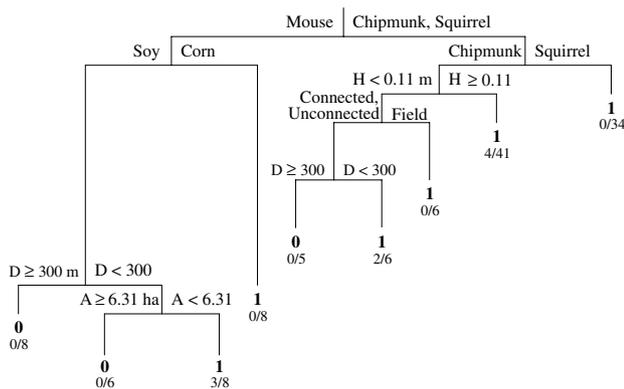

Fig. 6 – Classification tree for fate with weather variables and bearing excluded from the model. Terminal nodes represent multinomial measure of success: 1, never left corridor or field; 2, left but did not reach forest; 3, reached non-target patch; 4, reached target patch. The misclassification rate is provided below each node. Overall misclassification rate = 0.28. Abbreviations: A, area of target patch; D, release distance.

(misclassification rate = 21% and AUC = 0.81). Mice were successful when the matrix was corn. When the matrix was soybean, they were successful from distances less than 300 m and when the target patch was less than 6.3 ha. The model for fate performed poorly (misclassification rate = 38.5%) and predicted that when the matrix was corn, mice reached the target patch. When the matrix was soybean, the model predicted that mice did not reach a patch.

Chipmunks moved sooner from fields and unconnected corridors, and larger animals (>89 g) moved a day earlier. From connected corridors, movement was immediate when the release distance was less than 125 m. From greater distances, latency was less rapid when the matrix was composed of soybean, rather than corn ($R^2 = 0.413$). The model for success was excellent (misclassification rate = 8.6% and AUC = 0.94). When crops were low (<0.11 m), chipmunks were successful from fields. From corridors, they were successful from distances less than 300 m. When crops were tall, chipmunks successfully reached a forest patch from all distances except 650 m. This was an interesting artifact of the data. The node includes two misclassified successes. The remaining three failures include a confirmed predation event, and two suspected predation events. The classification tree for fate showed that when crops were present (>0.11 m), chipmunks reached the target patch (misclassification rate = 26.6%). Under low crops, they reached the target from fields, but they did not reach any patch from corridors.

The latency model for flying squirrels was very similar to the full model ($R^2 = 0.516$). Latency to move was longer when the target patch was small (<3.7 ha). When the target patch was larger, flying squirrels moved immediately from fields and unconnected corridors. In connected corridors, movement occurred sooner from greater distances (>175 m). Again, we could not develop a binomial model for success, as all flying squirrels reached a forest patch. The classification tree for

they were still successful from field release sites. But from corridors, they were successful only from distances less than 300 m.

The classification tree for the multinomial model of success performed equally to the full model (misclassification rate = 27.9%). Mice did not reach a forest patch when the matrix was soybean (Fig. 6). When the matrix was corn, mice reached the target patch from shorter distances (<212 m). From longer distances, they reached the target when it was less than 6.3 ha. Otherwise, they reached a non-target patch. Chipmunks and flying squirrels reached the target patch when it was greater than 1.2 ha. Otherwise, the model predicted that they stayed in the corridor or field.

In the species-specific regression tree, mice moved on average 3 nights earlier from fields and unconnected corridors than connected corridors ($R^2 = 0.456$). The classification tree for success performed slightly better than the full model

the multinomial model of success showed that flying squirrels did not leave the corridor when the target patch was small (<3.7 ha). When the target patch was larger, it was reached from fields and unconnected corridors. From connected corridors, it was reached from shorter distances (<175 m); otherwise, flying squirrels reached a non-target patch (misclassification rate = 13.2%).

4.   Discussion

We predicted species mobility through an agricultural matrix would show the following pattern: white-footed mouse ⩾ eastern chipmunk > southern flying squirrel. However, our study suggests an opposite pattern: southern flying squirrel ⩾ eastern chipmunk > white-footed mouse. The movement of animals in fragmented landscapes is thought to depend on their perception of landscape structure, their motivation, and the risks they are willing to incur (Bélisle, 2005). Our translocation experiments were designed to test whether agricultural fields are viewed as a barrier to movement (connected vs. unconnected corridors) and to attempt to quantify motivation (corridors vs. fields). We are not aware of any cues that would tell an animal whether a corridor is connected or unconnected, though such cues may certainly exist. Of all animals released in corridors that had not reached the forest in the first day or night, 86% in unconnected corridors had left the corridor and entered the matrix, whereas, only 24% of animals had left connected corridors. This suggests an ability to perceive whether they occupied a habitat isolate. It also is possible that animals performed exploratory movements within a corridor before we located them.

Additionally, most of the unconnected corridors to which we had access consisted of grasses, rather than trees or shrubs. The grouping of fields and unconnected corridors in nearly all of the classification and regression trees (only the connectivity tree for chipmunk success grouped the two corridors) indicates that grassy corridors were not perceived differently from fields. Although several mice and chipmunks used burrows in the grassy corridors, and one flying squirrel spent a day huddled in a clump of grass, it is likely that full-grown crops provided better cover than these corridors and were less intensively visited by predators (Gehring and Swihart, 2003). Because these corridors were unsuitable habitat, we are unable to elucidate whether these species willingly cross agricultural fields to disperse. However, the translocation data indicate that they certainly are capable of traversing fields. Moreover, movement towards non-target patches demonstrated even greater distances traversed through the matrix (mice: 1 km, chipmunks: 1.5 km, flying squirrels: 1.8 km).

Our results provide insight into what motivates movement decisions and contributes to successful movement. More immediate movement from fields and unconnected corridors than connected corridors suggests that mice, chipmunks, and flying squirrels were strongly motivated to find tree cover. Goheen et al. (2003) observed that tree squirrels were more likely to cross fields when crop cover was present, and they attributed this to a decrease in the perceived risk of predation. Although crop height did not interact with fields and uncon-

nected corridors in any of our models, the structural difference implies that fields and grassy corridors were perceived as more risky than treed corridors. Cottontail rabbits (*Sylvilagus floridanus*) and degus (*Octodon degus*) travel more quickly in open habitats (Bond et al., 2001; Vásquez et al., 2002), presumably, to avoid detection by predators. For those animals that reached a target patch, we analyzed the time it took them to reach the forest. Overall, the difference between the three release types was not significant ($F_{2,89} = 0.597$, $p = 0.55$), but animals spent on average half a day or night longer in connected treelines than in unconnected corridors and fields. Vigilance likely increased in open areas (Mahan and Yahner, 1999), but without foraging opportunities, it appears that movement through the matrix was faster.

Such compensatory behavior (*sensu* Rosenberg et al., 1998), moving faster, may have decreased the actual risk animals faced in the matrix, as there was no difference in predation rates between the matrix and corridors. Matter et al. (1996) found no difference in predation of mice and voles in fragmented and unfragmented landscapes, suggesting that avoidance of risky areas may be an innate response to habitat structure. If such behavior is innate, then forest rodents are unlikely to willingly enter the matrix to disperse. In the case of chipmunks, where we can compare corridors and fields, successful movement was more probable when there was crop cover. This finding suggests differential success of spring and fall dispersers. Spring dispersal occurs when fields are fallow, whereas crops in this region are at full height during fall dispersal. Thus, in the fall, the matrix may present a less imposing barrier. While connectivity models accounting for daily weather variation may not be feasible, incorporating seasonal variation of the landscape certainly is possible.

Motivation to move from connected corridors was influenced primarily by the size of the forest patch. When the target patch was less than 3 ha, animals tended to stay in the corridor. It is likely that mice and chipmunks perceived the treelines as suitable habitat; residency in structurally complex fencerows is well documented (Bennett et al., 1994; Merriam and Lanoue, 1990). Given that mice and chipmunks reach higher densities in smaller patches (Dooley and Bowers, 1996; Nupp and Swihart, 2000), it is possible that these species traveled towards the patch, but were unable to colonize, and thus, stayed in the corridor. However, according to the connectivity model, mice successfully reached forests less than 6 ha.

Flying squirrels were not attracted to small patches, which is consistent with a previous study in this region that documented occupancy only in large patches (Nupp and Swihart, 2000). Flying squirrels in this region have a thermoregulatory requirement to huddle in order to survive cold winters (Stapp et al., 1991). Energetic constraints are related to the pattern of range expansion of flying squirrels in Canada, where they have not colonized isolated patches (Bowman et al., 2005). We hypothesize that only large patches could sustain a population of flying squirrels over winter. Although we have not been able to test it here, we believe conspecific attraction associated with winter survival may be a strong motivator in flying squirrel dispersal.

Crop type influenced latency to move from connected treelines for chipmunks and flying squirrels, with shorter delays

in soybean fields. Corn may have provided a food source, whereas when surrounded by soybean fields, animals likely were more motivated to find food resources. Additionally, corn was an indicator of successful movement towards the target patch for mice. As the smallest species with the lowest perceptual range (Zollner and Lima, 1997), it is possible that mice simply followed the corn rows towards the forest edge, whereas soybean fields were more difficult to navigate. Another possibility is that they climbed corn stalks and hence increased their perceptual range.

Bearing was important in determining successful movement towards the target patch. Our measurement of bearing assumed that animals stayed on a straight search path in the first 12 h of movement. Modeling predicts that animals dispersing over long distances and through an inhospitable matrix should follow straighter paths (Zollner and Lima, 1999b). Siberian flying squirrels tend to move straight through the matrix (Selonen and Hanski, 2004), and mice and chipmunks have been observed to have path correlations (the correlation between directions of each step) of 0.85–0.96 (P. Zollner, personal communication). Homing animals often explore their surroundings with a series of forays in different directions, returning to the release site when home is not found (Bovet, 1990). It is possible that some animals initially moved in the wrong direction, then returned to the release site, in which case our assumption of straight movement and measurement of bearing after 12 h would be inaccurate. However, we would expect such forays would be common and observable. Of the 63 animals with a bearing greater than 10°, only 14 turned around on subsequent days to reach the target patch after initially heading in the wrong direction. Thus, the majority of animals did appear to maintain the same path. A nearly straight search strategy suggests that animals dispersing through novel, inhospitable areas encounter new habitat patches by chance. Exploratory movement prior to dispersal may allow animals to identify a target patch. However, Selonen and Hanski (2006) found that in the Siberian flying squirrel, long-distance dispersers explored less than short-distance dispersers. In fragmented landscapes, long-distance dispersal may be inescapable (Diffendorfer et al., 1995), and animals may be forced to forego exploratory movement. The importance of bearing also has implications for simulation models where random walks or other movement rules are employed (Bartumeus et al., 2005). When modeling rodent populations, highly correlated random walks may provide more accuracy.

Although our inclusion of weather variables in the dataset was motivated by field observations, we were surprised by their prevalence in the models. The recursive nature of building CART models demonstrates that the placement of weather variables at a particular node provided more explanatory power than any other variable. Rain (Fig. 7) and temperature were important factors in the latency to move for all species. Animals moved when conditions were clear, as we would expect. However, they also moved when conditions were poor, likely in response to a need to find better shelter. Weather has been described as important in insect dispersal, when wind may affect the ability to orient towards habitat (Schooley and Wiens, 2003). Weather variables also were found to correlate with dispersal in buzzards (Walls et al., 2005) and gos-
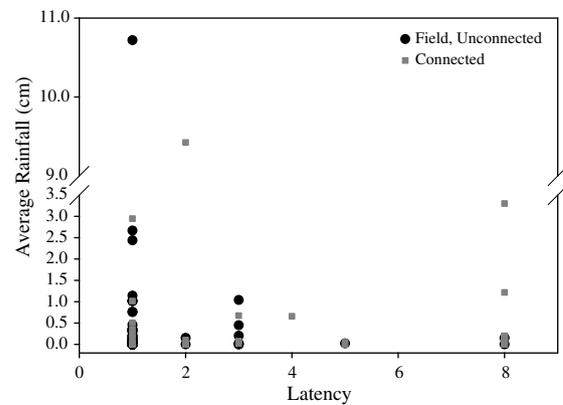

Fig. 7 – The relationship between rainfall and latency to move from connected corridors and unconnected corridors and fields by white-footed mice, eastern chipmunks, and southern flying squirrels. Animals were given 7 days to move. An 8 represents animals that did not move from the release site.

hawks (Wiens et al., 2006). Precipitation affects amphibian dispersal, making inhospitable habitat more permeable (Chan-McLeod, 2003). In mammals, weather has been correlated with seasonal migrations. For example, snow depth influences when white-tailed deer initiate movement (Brinkman et al., 2005). Weather also has been investigated in terms of demography (e.g. Schwartz and Armitage, 2005) and foraging behavior (Kotler et al., 1993; Orrock et al., 2004). However, we are unaware of studies documenting the effects of weather on short-term decisions related to mammalian dispersal. The full models, which included weather, performed as well or better than the connectivity models in the regression trees for latency with all species pooled and for each species separately. When small mammals are in inhospitable habitat, if no shelter is available, it is understandable that weather would influence movement. The full models had higher misclassification rates than the connectivity models for success and fate. Thus, weather probably had little to do with successful dispersal. However, animals may be more susceptible to mortality in adverse conditions, especially when energetic reserves are low. Some climate models predict an increased frequency of extreme weather events (National Assessment Synthesis Team, 2001). Therefore, investigating the combined effect of fragmentation and climate change on dispersal success would be a valuable endeavor (Opdam and Wascher, 2004).

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