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Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes*

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Abstract

Perceptual range is the maximum distance from which an animal can perceive the presence of remote landscape elements such as patches of habitat. Such perceptual abilities are of interest because they influence the probability that an animal will successfully disperse to a new patch in a landscape. Furthermore, understanding how perceptual range differs between species may help to explain differential species sensitivity to patch isolation. The objective of this research was to assess the perceptual range of eastern chipmunks (*Tamias striatus*), gray squirrels (*Sciurus carolinensis*), and fox squirrels (*Sciurus niger*) in fragmented agricultural landscapes. Animals were captured in remote woodlots and translocated to unfamiliar agricultural fields. There they were released at different distances from a woodlot and their movements towards or away from the woodlot were used to assess their ability to perceive forested habitat. Observed perceptual ranges of approximately 120 m for chipmunks, 300 m for gray squirrels, and 400 m for fox squirrels, suggest that differences in landscape-level perceptual abilities may influence the occurrence of these species in isolated habitat patches.

Introduction

Interspecific differences in patterns of landscape use often can be attributed to behavioral phenomena (Ims 1995). For example, habitat specialists may be reluctant to traverse large areas of matrix habitat (Laurance 1990; Rail et al. 1997; Heinen et al. 1998), and such behavior can affect the persistence of a fragmented population (Andren 1994; Laurance 1995; With and Crist 1995). Mortality risks during dispersal, as well as life history traits such as vagility and body size, may also influence the distribution of animals in fragmented landscapes (Taylor et al. 1993; Lidicker and Koenig 1996; Zollner and Lima 1999a). Indeed, several experiments have documented differential use of and movement through a common landscape by different species (With, 1994; Crist and Wiens 1995; Diffendorffer et al. 1995; With and Crist 1995, 1996; Wiens et al. 1997; Firle et al. 1998; Haddad 1999). Such differences can alter the dynamics and structure of populations (Crist and Wiens 1995), often increasing the susceptibility of isolated populations of poor dispersers to local extinction (Petterson 1985; Andren 1994). Thus, by refining our knowledge of what animals know about their surroundings and how they make decisions as they move through landscapes (Crist and Wiens 1995; Roitberg and Mangel 1997; Pither and Taylor 1998; Turchin 1998), we should increase our understanding of how the spatial configuration of habitat affects different species (Ims 1995; Gustafson and Gardner 1996; Zollner and Lima 1999a; Haddad 1999).

The ability of animals to perceive habitat at a distance is a behavioral mechanism that may be an important component of dispersal success in fragmented

landscapes (Lima and Zollner 1996; Zollner and Lima 1997). An animal's 'perceptual range' will determine the ease with which it can locate habitat patches and hence the time spent searching in a hostile matrix for such habitat (Zollner and Lima 1999a). Consequently, a species' sensitivity to habitat fragmentation may be to a great extent a function of its perceptual range. Unfortunately, empirical information on the perceptual abilities of vertebrates is rare and based on a few single species studies performed in different landscapes (Yoemans 1995; Zollner and Lima 1997; Andreassen et al. 1998; Gillis and Nams 1998; Zollner and Lima 1999c). Thus, a study comparing the perceptual abilities of several species within a common landscape and relating these abilities to each species occurance in isolated habitat patches should clarify the influence of perceptual range on dispersal success.

Forest-dwelling-sciurids have received considerable attention in studies of habitat fragmentation, and they appear to be sensitive to the effects of patch isolation (Henderson et al. 1985; Verboom and Van Apeldoorn 1990; Fitzgibbon 1993; Van Appeldoorn et al. 1994; Wauters et al. 1994; Sheperd and Swihart 1995; Rushton et al. 1997; Heinen et al. 1998). However, species may differ in their sensitivity to the effects of isolation, and these differences are likely to reflect a species' mobility in matrix habitat or some correlate such as body size (Swihart and Nupp 1998). Among the forest-dwelling sciurids of eastern North America, it is clear that gray squirrels (*Sciurus carolinensis*) are more sensitive to patch isolation than fox squirrels (*Sciurus niger*; Table 1). A third forest dwelling sciurid common to this area the eastern chipmunk (*Tamias striatus*) is also negatively effected by isolation of habitat (Table 1). However, the sensitivity of chipmunks to patch isolation relative to the other two species is unclear (Table 1). Working in east-central Illinois Rosenblatt et al. (1999) only found chipmunks in the three largest and best connected patches of ten which they surveyed, while gray and fox squirrels were present in six and nine patches respectively. However, Nupp and Swihart (1998) found chipmunks in all four patches that they surveyed in northwestern Indiana, including one patch that was 870 m from the nearest woodlot. More extensive surveys in northwestern Indiana indicate that chipmunks are less sensitive to patch isolation than either gray squirrels or fox squirrels (Nupp and Swihart in review). An assessment of the perceptual abilities of each of these three species should help clarify the role that perceptual range plays in influencing dispersal success in fragmented landscapes, as well as provide information on a mechanism that may contribute to observed difference in patterns of patch occupancy. Thus, the objective of this work was to examine the perceptual ranges of these three species, eastern chipmunks, eastern gray squirrels, and fox squirrels in fragmented agricultural landscapes of east central Illinois and west-central Indiana.

Methods

General methods

The ability of chipmunks and squirrels to orient towards forested habitat from a distance was used as a behavioral assay of their ability to perceive forested habitat at a distance. These abilities were assessed by capturing chipmunks and squirrels at distant woodlots and moving them to an unfamiliar, bare, fallow field, which was devoid of fence rows. At these novel fields animals were released at several distances (determined by pilot work; Zollner unpublished data) from the edge of a mature woodlot. The orientation of the movement path at each release distance was measured to assess perceptual range of each species (Zollner and Lima 1997; Zollner and Lima 1999c). Critical to this work is the assumption that the perception of a woodlot is equivalent to movement towards the woodlot. Few environments would appear as hostile to a chipmunk or squirrel as a barren field, and survival in such an environment requires locating forested habitat as soon as possible. Thus, it is reasonable to assume that if these animals perceived forested habitat they should have attempted to reach it.

I captured chipmunks with Sherman live traps and squirrels with Tomahawk live traps in mature woodlots 5–29 km from the release site. This 5 km minimum distance and movement barriers (roads, streams, etc.) between capture and release sites minimized the chance that animals had prior experience at the release site. I used adult males and females, and all pregnant or lactating females were excluded from the experiments. Traps were checked twice each day, once in the morning and once in the evening. Prior to their release, animals were provisioned with seeds and housed overnight in their traps in a small, unheated shed.

Releases were accomplished using a standard 'release mechanism'. The mechanism was constructed of a 40 cm long piece of PVC pipe that was either 6.5 cm (chipmunks) or 13 cm (squirrels) in diameter. A metal

Table 1. Reported sensitivities of three woodland *sciurids* to patch isolation.

Effect of patch isolation	Reference
Fox squirrels	
Fox squirrels were insensitive to levels of fragmentation in this study.	Nupp and Swihart (in review)
Fox squirrels were present in 31 of 37 patches surveyed and are apparently capable of crossing agricultural matrix.	
Wide distribution of fox squirrels (present in 9 out of 10 woodlots) indicates high mobility or prolonged persistence in isolated patches.	Rosenblatt et al. (1999)
Fox squirrels are ubiquitous in non-urban woodlots of row-crop dominated east central Illinois; attributed to their superior dispersal ability.	Rosenblatt (in review)
Relative to gray squirrels, fox squirrels move greater distances, and visit more patches when translocated.	
None of 49 radio-collared fox squirrels moved between isolated patches across agricultural matrix.	Sheperd and Swihart (1995)
Some fox squirrels did move 200–500 m away from woodlots through fencerows and one patch was colonized by a non-collared squirrel from at least 800 m away.	
Spatially explicit simulation found interpatch movements by fox squirrels were not constrained by patch isolation.	Swihart and Nupp (1998)
Empirical surveys found fox squirrels in all 18 patches examined even the most isolated ones.	
Gray squirrels	
Gray squirrels are less likely to be found in patches > 500 m from other woodlots and not connected by hedgerows.	Fitzgibbon (1993)
Sites that historically contained gray squirrels lost them as landscapes were reduced to less than 20% forested coverage.	Nixon et al. (1978)
Among 54 habitat variables analyzed, the best predictor of gray squirrel presence was the amount of forested habitat within 23.31 km^2 of a site.	
Gray squirrels were restricted to continuous forests and large sites (only present in 7 of 37 patches surveyed).	Nupp and Swihart (in review)
The best-fit logistic regression model of gray squirrel presence was positively associated with patch area and negatively associated with isolation.	
Gray squirrels were present in only 6 of 10 patches surveyed and were absent from isolated rural woodlots.	Rosenblatt et al. (1999)
Gray squirrels are restricted to towns and riparian forests in row-crop dominated east central Illinois, which was attributed to their hesitancy to move across open fields.	Rosenblatt (in review)
Relative to fox squirrels gray squirrels move shorter distances, and visit fewer patches when translocated.	
Successful introduction of gray squirrels to woodlots where they were absent for 20+ years supports the hypothesis that absence was maintained by isolation.	Rosenblatt (1999)
Spatially explicit simulation found interpatch movements by gray squirrels were constrained by patch isolation.	Swihart and Nupp (1998)
Empirical surveys found gray squirrels in 4 of 18 patches examined but not in the isolated ones.	

Table 1. Continued.

Effect of patch isolation	Reference
Eastern Chipmunks	
Eastern chipmunks reside in fencerows and use them as movement pathways between patches.	Bennett et al. (1994)
Two chipmunks were observed moving > 500 m between patches presumably through fencerows and numerous other long movements were documented within fencerows.	
One individual regularly crossed 70 m of open field.	Forsyth and Smith (1973)
Spatially explicit simulation found that patch connectivity was the most important factor determining persistence of eastern chipmunk populations in fragmented agricultural landscapes.	Henein et al. (1998)
Chipmunks were observed to move as far as 1560 m between woodlots and this travel was presumed to be largely through fencerows.	
	Henderson et al. (1985)
Chipmunks probably never crossed areas of matrix larger than 20–60 m although one individual may have moved as far as 460 m across fields.	
Eastern chipmunks were present in 4 out of 4 patches surveyed including one isolated patch.	Nupp and Swihart 1998
Chipmunks appear to be negatively influenced by forest fragmentation as survival rates for individuals living in patches were significantly lower than for those in continuous forest.	
Eastern chipmunks were present in 32 out of 37 patches and no significant model of presence/absence could be developed based on landscape metrics.	Nupp and Swihart (in review)
Chipmunks never crossed roads with clearances > 30 m and roadways > 90 m act as barriers.	Oxley et al. (1974)
Eastern chipmunks were only detected in large forest tracts that were well connected to other forested areas (3 out of 10 patches surveyed).	Rosenblatt et al. (1999)
Fencerows provide corridors for movements by chipmunks and reduce isolation of woodlots.	Wegner and Merriam (1979)
Chipmunks were never captured in agricultural fields.	

spike (30 cm long) was placed through two holes in the pipe at one end, and driven into the ground to secure the mechanism. This secured end of the pipe was covered with an opaque cap that prevented the animal from exiting the release mechanism. The other end of the pipe was left open until the animal was placed inside it, at which time the pipe was sealed with a plastic cap.

At the time of release, I transported chipmunks and squirrels to the study in opaque boxes that prevented them from visually assessing their surroundings. The actual release locations were placed in straight lines parallel to the edge of the woods at different distances from the woods for each species. Along these parallel lines the release sites were spaced such that no animals were released within 70 m of each other on any given day. At the release site, I removed animals from their traps and restrained them in either a heavy black cotton bag (chipmunks) or a wire handling cone (squirrels; Baumgartner 1940). Next, a unique tag was attached to an animal's ear. A tracking spool (1.7 g, 180 m, denier two-ply nylon No. 2 quilting bobbin; Barbour Threads Inc., Anniston, AL, USA) was then glued to the animal's back, and the loose end of this spool was tied to the release mechanism (Boonstra and Crane 1986; Key and Woods, 1996). I followed the spool-and-line technique described by Key and Woods (1996) with a few modifications: no animals used in this study were anaesthetized, and rather than wrapping tracking spools in adhesive tape, I placed them in small dark brown uninflated rubber ballons. After the spool was securely attached (20–30 s) each animal was lowered into the PVC pipe facing the back, and a plastic cap was placed over the open end of the pipe.

The release itself was done remotely from a distance of 60 m, so that my presence did not influence animal movements. This remote release was accomplished by pulling on a string, thereby removing the

plastic cap and opening one end of the release mechanism. After removing the caps, I immediately left the study site and did not return until the following day. While releasing animals and leaving the study site, I was at the same distance from the woods as the release mechanism, so my presence should not have biased the animals to move towards or away from the woods. Additionally, remote observations through a spotting scope during pilot work indicated that chipmunks and squirrels remained inside the release mechanism for 30–45 min after it was opened (P. A. Zollner pers. obs.).

The tracking spool left a trail of thread recording an animal's movements after it exited the release mechanism. The day following release, stick flags were placed in the ground along each thread trail at approximately 3 m intervals and at all points where the animal turned sharply. Each trail was followed until the thread ended or it reached the woods (chipmunks only). Trails that did not reach the woods were on average (±SE) 147.1 m (±3.6) long. Animals occasionally broke the thread before travelling the full 180 m although all trails included in these results exceeded 100 m in length. After tracking, I used a sighting compass (Brunton Sight Master 80NL) and field tape to measure the bearing and distance from the point of release to (i) each flag in the trail and (ii) the nearest point along the woodlot edge.

I assessed perceptual abilities by determining whether the animals' locations after traveling a prescribed distance (chipmunks 50 m; squirrels 100 m) were oriented towards the woods. These prescribed distances were shorter than the minimum distance to the woods (chipmunks 60 m, squirrels 300 m) but long enough to allow an animal to orient after dashing out of the release mechanism. The use of this minimum distance ensured that animals did not reach the woods as a result of random wandering (Goodwin et al. 1999; Zollner and Lima 1999b). The angle to each animals location after travelling the prescribed distance was calculated from the recorded movement pathways using trigonometry. V-tests were used to assess whether these angels were significantly oriented towards the woods for each species. The V-test is a modification of a Rayleigh test which examines whether observed angles are statistically clustered around a hypothesized angle (Batschelet 1981). I also used V-tests to determine whether the locations of the last points to which animals were tracked were oriented towards the home woodlot (site of capture). Furthermore, I examined the possibility of sex-related effects on angular orientations with Mardia-Watson-Wheeler (MWW) pairwise tests (Batschelet 1981). No test demonstrated any sex-related differences in orientation towards the woods (MWW test, $\chi^2 < 0.93$, d.f. $= 2$, $P > 0.1$), hence data from both sexes were combined before performing statistical analyses.

Species-specific methods

Eastern fox squirrels

During April–May, 1997, I captured 47 fox squirrels in a mature oak hickory woodlot in east-central Clark County, Illinois. These animals were released at a site 26 km away in north-central Edgar County, Illinois. This release site was a large 132-ha field bordered to the south by a second growth oak hickory forest, to the north by a road, and to the north, east and west by additional, large agricultural fields. Other than the forest along the southern edge of the release site, the nearest trees were 1.8 km away. All fox squirrels were released in this field between 10:00 and 14:00. Fox squirrels were released 300 m (15 squirrels), 500 m (16 squirrels), and 800 m (16 squirrels) from the forested southern edge of the field. During April–May, 1998, while studying gray squirrels (see below), I captured an additional 24 fox squirrels, which were released 300 m (8 squirrels), 400 m (8 squirrels) and 500 m (8 squirrels) from the forested southern edge of the field. These additional releases of fox squirrels allowed for the definition of fox squirrel perceptual range at the same scale used for gray squirrels (see below).

Gray squirrels

During April–May, 1998, I captured 28 gray squirrels in a mature oak hickory woodlot in south-central Clark County, Illinois. These squirrels were all of the gray color morph, although there is no reason to expect melanistic animals would have behaved differently (Gustafson and Van Druff 1990). These animals were released at the site used for the fox squirrel releases (see above), which was approximately 29 km away in Edgar County, Illinois. All gray squirrels were released between 10:00 and 14:00. Squirrels were released at 300 m (8 individuals), 400 m (10 individuals) and 500 m (10 individuals) from the forested southern edge of the field. Only 8 gray squirrels were released at 300 m because this species was difficult to capture locally, and it was apparent that they were orienting towards the woods from 300 m.

Eastern chipmunks

The chipmunk releases took place at two sites over the course of two different seasons. This was necessitated by difficulty in capturing enough animals in a single season and changes in the crop rotations between the years at the release sites. Tests indicated no difference between releases at these two sites, hence data were combined for all analyses (see below). Overall, 21 chipmunks were released 60 m from the woods, while 20 chipmunks were released at both 120 and 180 m from the woods.

During May 1996, I captured 22 chipmunks in a mature oak hickory woodlot in northwestern Vigo County, Indiana. These animals were released at a site 6.4 km away in west-central Vigo County. This release site was a 10-ha field bordered to the east by a mature oak hickory forest, to the north and south by additional agricultural fields and to the west by a road beyond which there were more agricultural fields. Other than the eastern edge of the release site, the nearest trees were 250 m away. As with the squirrels, all chipmunks were released between 10:00 and 14:00. Fourteen chipmunks were released 60 m and 8 chipmunks were released 120 m from the forested eastern edge of the field.

During October–November 1997, I captured 39 chipmunks in a mature oak hickory woodlot in eastern Clark County, Illinois. These animals were released at a site approximately 5 km away in central Clark County, Illinois. This release site was 7 km northwest of the release site used in 1996. The 1997 release site was a large 51 ha field bordered to the north by a mature oak hickory forest, to the east and west by additional fields and to the south by a road beyond which more fields were located. Other than the northern edge of the release site, the nearest other trees were 360 m away. All chipmunks were released in the field between 10:00 and 14:00. Chipmunks were released at 60 m (7 individuals), 120 m (12 individuals), and 180 m (20 individuals) from the forested northern edge of the field.

Results

Eastern fox squirrels

Releases conducted during 1997 demonstrated that the perceptual range of fox squirrels was between 300 and 500 m (Figure 1). The angular orientation of fox squirrels released 300 m from the woods was significantly oriented towards the woods (V-test: $u = 4.93$, $P < 0.0001$). In contrast, fox squirrels released at 500 or 800 m from the woods were not significantly oriented towards the woods (500 m releases, V-test: $u = -1.25$, $P > 0.1$; 800 m releases, V-test: $u = -0.03$, $P > 0.1$).

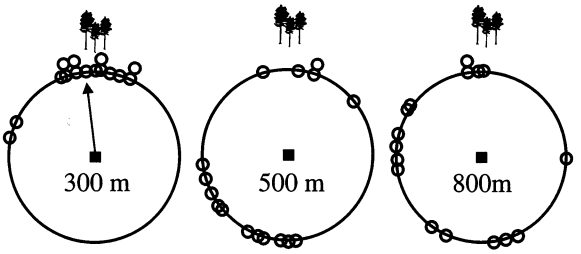

Figure 1. Angular orientations of fox squirrels released during 1997. Fox squirrels were released 300, 500, and 800 m from the woods; angular orientations were assessed after 100 m of travel. The solid square in the center of each panel represents the site where animals were released and the trees show the direction to the woods. The angular orientation of each fox squirrel is depicted as an open circle on the unit circle. Vectors indicate average angle and degree of orientation and are displayed only for cases with statistically significant orientation towards the woods.

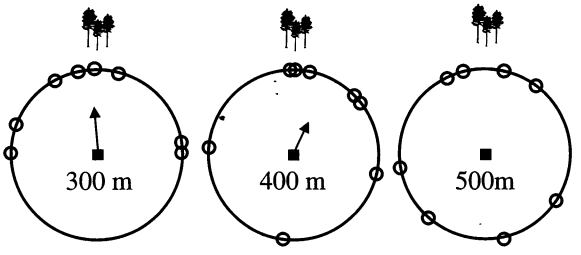

Figure 2. Angular orientations of fox squirrels released during 1998. Fox squirrels were released 300, 400, and 500 m from the woods; and angular orientations were assessed after 100 m of travel. All symbols are as in Figure 1.

Releases conducted during 1998 suggest that the perceptual range of fox squirrels was between 400 and 500 m (Figure 2). The angular orientation of fox squirrels released 300 m from the woods was significantly oriented towards the woods (V-test: $u = 2.23$, $P < 0.01$). Fox squirrels released 400 m from the woods were marginally oriented towards the woods (V-test: $u = 1.58$, $P = 0.0594$). Recall that because of logistic constraints only 8 animals were released at this treatment distance. Thus, it is likely that a greater sample size may have made this orientation more apparent. Fox squirrels released 500 m from the woods were not oriented towards the woods (V-test: $u = 1.18$, $P > 0.1$).

Fox squirrels were released 300 and 500 m from the woods during both 1997 and 1998. Mardia–Watson–Wheeler pairwise comparisons of fox squirrel

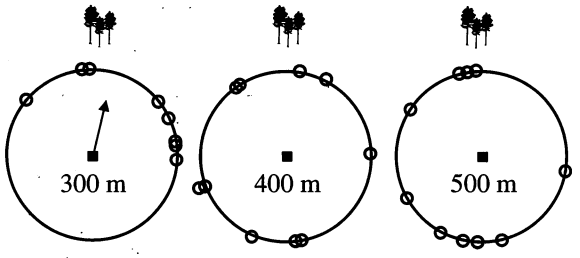

Figure 3. Angular orientations of gray squirrels released during 1998. Gray squirrels were released 300, 400, and 500 m from the woods; and angular orientations were assessed after 100 m of travel. All symbols are as in Figure 1.

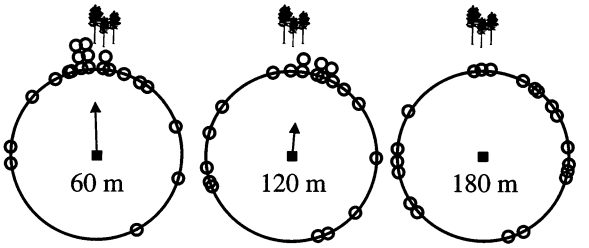

Figure 4. Angular orientations of chipmunks released during 1996 and 1997 (see text). Chipmunks were released 60, 120, and 180 m from the woods; and angular orientations were assessed after 50 m of travel. All symbols are as in Figure 1.

data found no year-specific difference in the angular orientations of fox squirrels released at 300 m (MWW test, $\chi^2 = 3.01$, d.f. = 2, $P > 0.1$) or 500 m (MWW test, $\chi^2 = 3.71$, d.f. = 2, $P > 0.1$) from the forest edge. After combining the data from the two years, fox squirrels released 300 m from the woods were still significantly oriented towards the woods (V-test: $u = 5.29$, $P < 0.0001$), while fox squirrels released 500 m from the woods still were not (500 m fox squirrels, V-test: $u = -3.42$, $P > 0.1$). Finally, fox squirrels not significantly oriented towards the woods failed to show significant orientation towards the site where they were captured (500 m releases, V-tests, $u = 0.51$, $P > 0.1$; 800 m releases, V-tests, $u = -0.15$, $P > 0.1$).

Gray squirrels

The perceptual range of gray squirrels was between 300 and 400 m (Figure 3). Gray squirrels released 300 m from the woods were significantly oriented towards the woods (V-test: $u = 2.85$, $P < 0.005$). In contrast, gray squirrels released 400 or 500 m from the woods were not significantly oriented towards the woods (400 m releases, V-test: $u = -0.05$, $P > 0.1$; 500 m releases, V-test: $u = -0.46$, $P > 0.1$). Finally, gray squirrels not significantly oriented towards the woods also failed to show a significant orientation towards the site at which they were captured (400 m releases, V-test, $u = 0.06$, $P > 0.1$; 500 m releases, V-test, $u = 0.32$, $P > 0.1$).

Eastern chipmunks

Recall that circumstances dictated the use of two sites over two field seasons for the chipmunk releases (see above). Mardia–Watson–Wheeler pairwise comparisons of chipmunk locations found no site-specific differences in the angular orientations of chipmunks released at 60 m (MWW test, $\chi^2 = 1.49$, d.f. = 2, $P > 0.1$) or 120 m (MWW test, $\chi^2 = 5.06$, d.f. = 2, $P > 0.1$) from the forest edge. Thus, data from each site were pooled for chipmunks released at 60 and 120 m during all subsequent analyses; all 180 m releases were done at the second site.

The perceptual range of eastern chipmunks was between 120 m and 180 m (Figure 4). The locations of chipmunks were significantly oriented towards the woods for animals released either 60 or 120 m from the woods (60 m releases, V-test: $u = 4.26$, $P < 0.0001$; 120 releases, V-test: $u = 2.64$, $P < 0.005$). In contrast, chipmunks released 180 m away were not oriented towards the woods (V-test: $u = 0.82$, $P > 0.1$); these chipmunks also failed to show a significant orientation towards the site at which they were captured (V-test, $u = 0.81$, $P > 0.1$).

Discussion

Consistent with the hypothesis that perceptual range influences dispersal success and thus the way animals use landscapes, the perceptual range of gray squirrels, was less than that of fox squirrels. This ordering of perceptual ranges is inversely related to the reported sensitivities of these two species to habitat isolation (Table 1), which suggests that differences in perceptual abilities contribute to the occurrences of these species in fragmented agricultural landscapes. Proximately, the differences in the perceptual abilities of these species may also be related to differences in body size (Gillis and Nams 1998). The ultimate origin of these differences in perceptual abilities may be related to historical differences in habitat occupied by these species. Historically, fox squirrels were common at the interface of the eastern deciduous forests and the prairie, while gray squirrels were found in interior forest habitat (Allen 1943; Smith and Follmer 1972;

Swihart and Nupp 1998). Fox squirrels presumably have a longer evolutionary history with large areas of open habitat, while gray squirrels have been exposed to open habitat only since the recent clearing of forests for agriculture. This is consistent with the observation that fox squirrels forage as 'patch transients' while gray squirrels forage as 'patch residents' (Steele and Weigl 1992).

The observed perceptual range of chipmunks suggests they should be more sensitive to the effect of fragmentation than either squirrel species, but dispersal success is likely to be influenced by a variety of factors (see below). Chipmunks clearly are sensitive to the effects of habitat isolation (Wegner and Merriam 1979; Henderson et al. 1985; Heinen et al. 1998; Nupp and Swihart 1998; Rosenblatt et al. 1999), however their sensitivity relative to that of the squirrels remains unresolved (Rosenblatt et al. 1999; Nupp and Swihart in review). This ambiguity may in part be attributable to differences between study sites such as the proportion of the landscape containing forested habitat, the quality of the habitat for chipmunks, or the range of isolation values investigated. Additional factors such as the occurrence of fence rows in these landscapes might confound comparisons because fence rows containing resident populations of chipmunks (Bennett et al. 1994) may not be included in calculations of patch isolation. Finally, differences might also be attributable to geographic variation in either historical habitat or land use patterns. Note that the perceptual ranges reported here are consistent with the sensitivities to patch isolation observed by Rosenblatt et al. (1999) who's work occurred in close geographic proximity to these study sites.

The perceptual range which each of these species effectively experience during dispersal may not always be as great as the values reported here. All three of these species are known to disperse during times of the year when crops are present in the fields, and visually obstructive crops may reduce the ability to perceive distant habitat (Zollner and Lima 1997). Animals might minimize the perceptual constraints which crops impose by climbing trees prior to dispersal, but any such gains would only apply to the immediate vicinity of their point of origin and not their entire search path (Zollner and Lima 1999c). Furthermore, dispersal is typically done by juveniles which may have more limited perceptual ranges than the adults used in these experiments (Zollner unpublished data). Nonetheless, the estimates presented here are likely to be good approximations of the maximum perceptual range for each of these species.

Perceptual range influences dispersal success most when species face an intermediate probability of successful dispersal. Fahrig (1988) demonstrated this pattern for simulated animals facing different proportions of suitable habitat in a landscape. This same principle is likely to apply to other factors that affect dispersal success. For example, species using highly effective search strategies will find patches quickly no matter what their perceptual range (Zollner and Lima 1999a). Alternatively, species facing very high mortality risks may never successfully disperse because they will die before reaching new habitat even when endowed with vast perceptual abilities (Swihart and Nupp 1998). Such differences may explain why some simulations have found dispersal success to be sensitive to perceptual range (Fahrig 1988; Pulliam et al. 1992; Turner et al. 1993) while others have indicated that perceptual range is inconsequential (Liu et al. 1995; Swihart and Nupp 1988).

A key assumption in this experiment was that if the animals could perceive forested habitat they would move towards it. This is a reasonable assumption since all of these species are woodland resident animals (Snyder 1982; Koprowski 1994a, 1994b) that face an increased risk of predation in open habitat (Bowers and Ellis 1993; Bowers et al. 1993; Lima 1998). This increase in risk is demonstrated by the observation that all of these species will forage in open fields, but only when they are close to forested habitat or other cover (Lima and Valone 1986; Sheperd and Swihart 1995; McAdam and Kramer 1998). Further support for this assumption was provided by the observation that several chipmunks released at 180 m actually dug shallow tunnels, presumably to reduce their risk of predation while lost. In contrast, chipmunks released at 60 and 120 m moved directly towards the woods and never dug such tunnels. This protocol also assumed that the release sites were unfamiliar to the subjects. This assumption is supported by several lines of evidence: (i) all translocation distances exceeded reported homing abilities of all species (Hungerford and Wilder 1941; Seidel 1961; Bendel and Therres 1994); (ii) no homeward orientation was detected for any of these releases; and (iii) no marked animals were recaptured at trapping sites. Finally, pilot observations indicate that animals remain in the release mechanisms for at least 0.5 hours after the cap is removed. Thus distress caused by handling the animals (Goodwin et al. 1999) should have subsided prior to the recorded move-

ments. Furthermore, such stress should only increase the desire of these woodland resident animals to move towards the forest if they perceive it (Zollner and Lima 1999b).

Perceptual range is certainly not the only factor affecting dispersal success. Landscape characteristics such as the presence of fence rows or the composition of the matrix may be important for dispersing chipmunks and squirrels (Wegner and Merriam 1979; Fitzgibbon 1993; Bennett et al. 1994; Sheperd and Swihart 1995). Mortality risks are also known to increase during dispersal (Larsen and Boutin 1994; Van Vuren 1998), and chipmunks and squirrels may face different mortality risks while moving through agricultural fields (Smith and Follmer 1972; Swihart and Nupp 1998). Such differences in mortality would determine the best dispersal search strategy (Zollner and Lima 1999a), and even the willingness of animals to cross matrix habitat (Lidicker and Koenig 1996). Additionally, factors such as energetic reserves (Nunes and Holekamp 1996) and social conditions (Nixon et al. 1986) are likely to influence dispersal decisions and success. Clearly, dispersal success is affected by a wide variety of behavioral attributes and landscape components (Wiens et al. 1997), and we have only a minimal understanding of the relative contribution of these different elements to dispersal success.

In summary, the perceptual abilities of eastern chipmunks, gray squirrels, and fox squirrels suggest that perceptual range may contribute to dispersal success for these species in agriculturally fragmented landscapes. Certainly, other behaviors are also likely to influence dispersal success and thus warrant further investigation with the comparative approach used in this paper. A series of such investigations could be used to parameterize spatially explicit simulation models and perform sensitivity analysis, greatly increasing our understanding of which behavioral characteristics influence dispersal success to what extent. Thus, the present study is an important step towards the development of a more general understanding of how behavioral processes influence patterns of distribution across landscapes. Ultimately, this understanding is of interest because of the role that dispersal success plays in maintaining viable populations in fragmented landscapes (Andren 1994; With and Crist 1995).

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References

Allen, D.L. 1943. Michigan fox squirrel management. Dept. of Cons., Game Div. Publ. 100: 1–404.

Andreassen, H.P., Bjornbom, E., Carlson, R.G., Gunderson, G. and Gunderson, H. 1998. Visual cues as determinants of perceptual range in root voles *Microtus oeconmus*. Acta Theriologica 43: 371–378.

Andren, H. 1994. Effects of habitat fragmentation on birds and mammals in landscapes with different proportions of suitable habitat: a review. Oikos 71: 355–363.

Batschelet, E. 1981. Circular Statistics in Biology. Academic Press, New York, NY, USA.

Baumgartner, L.L. 1940. Trapping, handling, and marking fox squirrels. J. Wildl. Manage. 4: 479–484.

Bennett, A.F., Henein, K. and Merriam, G. 1994. Corridor use and the elements of corridor quality: chipmunks and fencerows in a farmland mosaic. Biol. Cons. 68: 155–165.

Bendel, P.R. and Therres, G.D. 1994. Movements, site fidelity and survival of Delmarva fox squirrels following translocation. Am. Midl. Nat. 132: 227–233.

Boonstra, R. and Craine, I.T.M. 1986. Natal nest location and small mammal tracking with a spool and line technique. Can. J. Zool. 64: 1034–1036.

Bowers, M.A. and Ellis, A. 1993. Load size variation in the eastern chipmunk, *Tamias striatus*: the importance of distance from burrow and canopy cover. Ethology 94: 72–82.

Bowers, M.A., Jefferson, J.L. and Kuebler, M.G. 1993. Variation in giving up densities of foraging chipmunks (*Tamiais striatus*) and squirrels (*Sciurus carolinensis*). Oikos 66: 229–236.

Crist, T.O. and Wiens, J.A. 1995. Individual movements and estimation of population size in darkling beetles (Coleoptera: Tenebrionidae). J. Anim. Ecol. 64: 733–746.

Diffendorfer, J.E., Gaines, M.S. and Holt, R.D. 1995. Habitat fragmentation and movements of three small mammals (*Sigmodon*, *Mocrotus*, and *Peromyscus*). Ecology. 76: 827–839.

Fahrig, L. 1988. A general model of populations in patchy habitats. Appl. Math. C. 27: 53–66.

Firle, S., Bommarco, R., Ekbom, R. and Natiello, M. 1998. The influence of movement and resting behavior on the range of three carabid beetles. Ecology 79: 2113–2122.

Fitzgibbon, C.D. 1993. The distribution of grey squirrel dreys in farm woodland: the influence of wood area, isolation and management. J. Appl. Ecol. 30: 736–742.

Forsyth, D.J., and Smith, D.A. 1973. Temporal variability in home ranges of eastern chipmunks (*Tamias striatus*) in a South-eastern Ontario woodlot. Am. Midl. Nat. 90: 107–117.

Goodwin, B.J., Bender, D.J., Contreras, T.A., Fahrig L. and Wegner, J.F. 1999. Testing for habitat detection distances using orientation data. Oikos, 84: 160–163.

Gillis, E.A. and Nams, V.O. 1998. How red backed voles find habitat patches. Can. J. Zool. 76: 791–794.

Gustafson, E.J. and Gardner, R.H. 1996. The effect of landscape heterogeneity on the probability of patch colonization. Ecology 77: 94–107.

Gustafson, E.J. and Van Druff, L.W. 1990. Behavior of black and gray morphs of *Sciuris carolinensis* in an urban environment. Am. Midl. Nat. 123: 186–192.

Haddad, N.M. 1999. Corridor use predicted from behaviors at habitat boundaries. Amer. Nat. 153: 215–227.

Henderson, M.T., Merriam G. and Wegner, J. 1985. Patchy environments and species survival: chipmunks in an agricultural mosaic. Biol. Conserv. 31: 95–105.

Henein, K., Wegner, J. and Merriam, G. 1998. Population effects of landscape model manipulation on two behaviourally different woodland small mammals. Oikos 81: 168–186.

Hungerford, K.E. and Wilder, N.G. 1941. Observations on the homing behavior of the gray squirrel (*Sciurus carolinensis*). J. Wildl. Manage. 5: 458–460.

Ims, R.A. 1995. Movement patterns related to spatial structures. *In* Mosaic landscapes and cological rocesses. pp. 85–109. Edited by L. Hansson, Fahrig, L. and Merriam, G. Chapman and Hall, London.

Key, G.E. and Woods, R.D. 1996. Spool-and-line studies on the behavioural ecology of rats (*Rattus* spp.) in the Galapagos Islands. Can. J. Zool. 74: 733–737.

Koprowski, J.L. 1994a. *Sciurus niger*. Mammalian Species Account 479: 1–9.

Koprowski, J.L. 1994b. *Sciurus carolinensis*. Mammalian Species Account 480: 1–9.

Larsen, K.W. and Boutin, S. 1994. Movements, survival, and settlement of red squirrel (*Tamiasciurus hudsonicus*) offspring. Ecology 75: 214–223.

Laurance, W.F. 1995. Extinction and survival of rainforest mammals in a fragmented tropical landscape. *In* Landscape approaches in mammalian ecology and conservation. pp. 46–63. Edited by W.Z. Lidicker, Jr. University of Minnesota Press, Minneapolis.

Laurance, W.F. 1990. Comparative responses of five arboreal marsupials to tropical forest fragmentation. J. Mammal. 71: 641–53.

Lidicker, W.Z., Jr. and Koenig, W.D. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. *In* Metapopulations and wildlife conservation. pp. 85–111. Edited by D.R. McCullough. Island Press, Washington D.C.

Lima, S.L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. Adv. Study Behav. 27: 215–290.

Lima, S.L. and Zollner, P.A. 1996. Towards a behavioral ecology of ecological landscapes. Trends Ecol. Evol. 11(3): 131–135.

Lima, S.L. and Valone, T.J. 1986. Influence of predation risk on diet selection: a simple experiment in the gray squirrel. Animal Behav. 34: 536–544.

Liu, J., Dunning, J.B. and Pulliam, H.R. 1995. Population effects of a forest management plan on Bachman's sparrows (*Aimophila aestivalis*): linking a spatially-explicit model with GIS. Conserv. Biol. 9: 62–75.

McAdam, G. and Krammer, D.L. 1998. Vigilance as a benefit of intermittent locomotion in small mammals. Animal Behav. 55: 109–117.

Nixon, C.M., Havera, S.P. and Greenberg, R.E. 1978. Distribution and abundance of the gray squirrel in Illinois. Illinois Natural History Survey Biological Notes, Vol. 105, 55p.

Nixon, C.M., Hansen, L.P. and Havera, S.P. 1986. Demographic characteristics of an unexploited population of fox squirrels (Sciurus niger). Can. J. Zool. 64: 512–521.

Nunes, S. and Holekamp, K.E. 1996. Mass and fat influence timing of natal dispersal in Belding's ground squirrels. J. Mammal. 77: 807–817.

Nupp. T.E. and Swihart, R.K. 1998. Effects of forest fragmentation on population dynamics of white-footed mice and eastern chipmunks. J. Mammal. 79: 1234–1243.

Nupp. T.E. and Swihart, R.K. in review. Landscape-level correlates of small mammal assemblages in forest fragments of farmlands. J. Mammal.

Pettersson, B. 1985. Extinction of an isolated population of the middle spotted woodpecker *Dendrocopos medius* (L.) in Sweden and its relation to general theories on extinction. Biol. Conserv. 32: 335–353.

Pither, J. and Taylor, P.D. 1998. An experimental assessment of landscape connectivity. Oikos 83: 166–174.

Pulliam, H.R., Dunning, J.B. Jr. and Liu, J. 1992. Population dynamics in complex landscapes: a case study. Ecol. Appl. 2: 165–177.

Oxley, D.J., Fenton, M.B. and Carmody, G.R. 1974. The effects of roads on populations of small mammals. J. Appl. Ecol. 18: 51–59.

Rail, J-F., M. Darveau, A. Desrochers, and J. Huot. 1997. Territorial responses of boreal forest birds to habitat gaps. Condor 99: 976–980.

Roitberg, B.D. and Mangel, M. 1997. Individuals on the landscape: behavior can mitigate landscape differences among habitats. Oikos 80: 234–240.

Rosenblatt, D.L. in review. An experimental examination of tree squirrel vagility in an agricultural landscape. Landscape Ecol.

Rosenblatt, D.L. 1999. The effect of habitat fragmentation on forest mammals: An experiemntal analysis of tree squirrel distributions in the agricultural landscape of east central Illinois. Unpublished Ph.D. Dissertation, University of Illinois, Urbana, Illinois.

Rosenblatt, D.L., Heske, E.J., Nelson, S.L., Barber, D.M., Miller, M.A. and MacAllister, B. 1999. Forest fragments in east-central Illinois: island or habitat patches for mammals? Am. Midl. Nat. 141: 115–123.

Rushton, S.P., Lurz, P.W.W., Fuller, R. and Garson, P.J. 1997. Modelling the distribution of the red and grey squirrel at the landscape scale: a combined GIS and population dynamics approach. J. Appl. Ecol. 34: 1137–1154.

Seidel, D.R. 1961. Homing in the eastern chipmunk. J. Mammal. 42: 256–257.

Sheperd, B.F. and Swihart, R.K. 1995. Spatial dynamics of fox squirrels (*Sciurus niger*) in fragmented landscapes. Can. J. Zool. 73: 2098–2105.

Smith, C.C. and Folmer, D. 1972. Food preferences of squirrels. Ecology 53: 82–91.

Snyder, D.P. 1982. *Tamias striatus*. Mammalian Species Account. 168: 1–8.

Steele, M.A. and Weigl, P.D. 1992. Energetics and patch use in the fox squirrel *Sciurus niger*: response to variation in prey profitability and patch density. Am. Midl. Nat. 128: 156–167.

Swihart, R.K. and Nupp, T.E. 1998. Modeling population responses of North American tree squirrels to agriculturally-induced fragmentation of forests. *In Ecology and evolutionary biology of tree squirrels*. pp. 1–19. Edited by M.A. Steele, Merritt J.F. and

Zegers, D.A. Special Publication, Virginia Museum of Natural History, Vol. 6.

Taylor, P.D., Fahrig, L., Henein, K. and Merriam, G. 1993. Connectivity is a vital element of landscape structure. Oikos 68: 571–573.

Turchin, P. 1998. Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants. Sinauer Associates, Sunderland, Mass.

Turner, M.G., Wu, Y., Romme, W.H. and Wallace, L.L. 1993. A landscape simulation model of winter foraging by large ungulates. Ecol. Model. 69: 163–184.

Van Appeldoorn, R.C., Celada, C. and Nieuwenhuizen, W. 1994. Distribution and dynmaics of the red squirrel (*Sciurus vulgaris L.*). Landscape Ecol. 9: 227–235.

Van Vuren, D. 1998. Mammalian dispersal and reserve design. *In* Behavioral ecology and conservation biology. pp. 369–393. Edited by T.M. Caro. Oxford University Press, Oxford.

Verboom, B. and Van Apeldoorn, R. 1990. Effects of habitat fragmentation on the red squirrel, *Sciurus vulgaris* L. Landscape Ecol. 4: 171–176.

Wauters, L., Casale, P. and Dhondt, A.A. 1994. Space use and dispersal of red squirrels in fragmented habitats. Oikos 69: 140–146.

Wegner, J.F. and Merriam, G. 1979. Movements by birds and small mammals between a wood and adjoining farmland habitats. J. Appl. Ecol. 16: 349–357.

Wiens, J.A., Schooley, R.L. and Weeks, R.L., Jr. 1997. Patchy landscapes and animal movements: do beetles percolate? Oikos 78: 257–264.

With, K.A. 1994. Using fractal analysis to asses how species perceive landscape structure. Landscape Ecol. 9: 25–36.

With, K.A. and Crist, T.A. 1995. Critical thresholds in species' responses to landscape structure. Ecology 76: 2446–2459.

With, K.A. and Crist, T.O. 1996. Translating across scales: simulating species distributions as the aggregate response of individuals to heterogeneity. Ecol. Model. 93: 125–137.

Yoemans, S.R. 1995. Water-finding in adult turtles: random search or oriented behaviour? Anim. Behav. 49:977–987.

Zollner, P.A. and Lima, S.L. 1997. Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat. Oikos 80: 51–60.

Zollner, P.A. and Lima, S.L. 1999a. Search strategies for landscape-level inter-patch movements. Ecology 80: 1019–1030.

Zollner, P.A. and Lima, S.L. 1999b. Orientational data and perceptual range: real mice aren't blind. Oikos 84: 164–166.

Zollner, P.A. and Lima, S.L. 1999c. Illumination and the perception of remote habitat patches by white-footed mice. Anim. Behav. 58: 489–500.