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Landscape-level perceptual abilities in white-footed mice: perceptual range and the detection of forested habitat

Patrick A. Zollner and Steven L. Lima

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We define perceptual range as the distance from which an animal can perceive key landscape elements, such as distant patches of forested habitat. We argue that perceptual range should be a determinant of not only dispersal success in unfamiliar or hostile landscapes, but also of several landscape-level ecological processes influencing population dynamics. To redress the absence of empirical information on perceptual ranges, we simulated the dispersal of forest-dwelling white-footed mice (*Peromyscus leucopus*) across an agricultural landscape by releasing mice into unfamiliar, hostile agricultural habitat at various distances from fragments of forested habitat. We found that these forest mice have a remarkably low perceptual range with regard to detecting their forested (core) habitat. Mice released into bare fields failed to even orient towards forested habitat as little as 30 m distant, while mice in crop fields appeared unable to locate forest habitat as little as 10 m distant. These mice seemed to locate forested habitat by vision, despite the availability of non-visual cues. Future work will undoubtedly demonstrate vast differences in landscape-level perceptual abilities among animals, and show clearly that the ecological effects of a given landscape configuration will be influenced by the behavioral attributes of the species in question.

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This study addresses the ability of animals to perceive key elements of the ecological landscape in which they live. Specifically, we examine the “perceptual range” of the white-footed mouse (*Peromyscus leucopus*) regarding the detection-at-a-distance of forested landscape elements (woodlots) within an agricultural landscape mosaic. We believe that an understanding of an animal’s perceptual range will not only shed light on its population dynamics in fragmented landscapes (Lima and Zollner 1996), but also emphasize that ecological landscapes themselves should be defined with respect to the behavioral attributes of the animals in question (Merriam 1991, Johnson et al 1992, Wiens et al. 1993, With 1994).

We envision the link between the perceptual abilities and population dynamics as being mediated through the elevated risk of mortality experienced by dispersing animals (e.g., Clarke et al. 1993, Larsen and Boutin 1994, Waser et al. 1994). Simply put, an animal with a low perceptual range will experience a relatively high risk of mortality, as it will spend more time searching for a suitable habitat patch than would one with a high perceptual range (Gaines and McClenaghan 1980, Doak et al. 1992). Fahrig (1988) and Turner et al. (1993) demonstrate theoretically that perceptual range may indeed be an important determinant of population dynamics (but see also Turner et al. 1994, Liu et al. 1995).

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However, few theoretical studies investigate the effects of perceptual abilities on population dynamics (Lima and Zollner 1996), despite the fact that a perceptual range of some sort appears in many landscape-explicit population models (Fahrig 1988, Saarenmaa et al. 1988, Danielson 1991, 1992, Doak et al. 1992, Pulliam et al. 1992, Turner et al. 1993, 1994, Adler and Nuernberger 1994, Liu et al. 1997).

How well can animals perceive the various features of ecological landscapes? There is remarkably little empirical information on the perceptual range of any vertebrate regarding the remote detection of landscape elements (Lima and Zollner 1996); Yoemans (1995) provides a notable exception in a study on aquatic turtles. Many insects and other arthropods appear to have only a limited ability to detect habitat patches visually (Hoffmann 1983, Kareiva 1985, Fahrig and Paloheimo 1987, Capman et al. 1990; but see Parmenter et al. 1989), but may detect habitat patches by olfaction at a considerable distance (see Nottingham 1988).

Our experiments focused on the ability of white-footed mice to perceive forest fragments while traveling in the agricultural matrix within which these fragments are imbedded. We chose to study white-footed mice as they (and congeners) are prominent in studies of landscape-level ecological phenomena (e.g., Fahrig and Merriam 1985, Morris 1987, Merriam and Lanoue 1990, Bowers and Dooley 1991, 1993) and in studies of homing, navigation, and dispersal (e.g., Drickamer and Stuart 1984, Anderson 1989, Teferi and Millar 1993). We examined the perceptual abilities of these mice in both bare (fallow) and soybean fields. The results from these two habitats are presented separately in the following sections, and show in each case a surprisingly limited perceptual range.

Perceptual abilities in bare fields

Rationale

Our experimental approach simulated the situation faced by white-footed mice as they disperse into an unfamiliar landscape (cf. Merriam and Lanoue 1990). This involved capturing mice from a remote location and releasing them in an bare, fallow field at various distances from the edge of a mature woodlot. The ability of white-footed mice to locate or orient towards the woodlot was used as an indication of their perceptual abilities relative to forested habitat.

Critical to this work is the assumption that the perception (or detection) of a woodlot is equivalent to behavioral action oriented towards the woodlot. This is a reasonable assumption: few environments would appear as hostile to a forest mouse as a barren field. We address further the validity of this assumption in a following section.

Methods

Study site

This experiment took place in western Indiana (Vigo County), USA, from April through May, 1994. The main study site, or release site, was a level, 22-ha, rectangular agricultural field bordered immediately to the north by a 115-ha mature hardwood forest (approximately 16 m in height), and to the west by a larger field. The southern and eastern edges of the study site were bordered by paved roads, beyond the road to the south was a second field; beyond the road to the east was more forest. This field had been planted in soybeans the previous summer, and then plowed and leveled the previous fall. The field was thus devoid of vegetative cover or furrows.

Capture and handling

White-footed mice were captured in a mature woodlot 5 km southeast of the release site. The 5 km distance between sites of capture and release minimized the chance that mice had any prior experience at the release site. Mice were trapped with Sherman live traps that were checked every morning. White-footed mice were distinguished from deer mice (*P. maniculatus bairdii*) as per Whitaker (1982). Only adult white-footed mice (both sexes) were used in these experiments. Captured white-footed mice were transported in their traps to a small, unheated shed at the release site, which housed mice during the daylight period before their release (the following night). Each mouse was provisioned with black oil sunflower seeds to sustain them until release.

Release

Mice were released the night after their capture; the exact mode of release is described below. Mice were released well after civil twilight (i.e. when the sun is more than 6° below the horizon; Mitton 1991) on moonless or cloudy nights. Releases were done at 10, 20 or 30 m from the edge of the woods adjoining the release site; there was no other woody vegetation within 350 m of any release location. Actual release locations were spread uniformly relative to the edge of the woods. The 300-m-long wooded edge allowed release sites to be spaced such that no animals were released within 50 m of each other on any given night. No mice were released at a given location until rain had removed existing fluorescent trails. This rain should also have minimized or removed any potential cues left by previously released mice. Twenty mice were released at each of the 3 release distances. Captured mice were assigned randomly to a given release distance. Mice released at distances of 10, 20, and 30 m faced respective forest horizon angles of approximately 57, 38, and 28° (assuming a 16 m high forest).

The actual release of a mouse was accomplished using a standard "release mechanism". This mechanism

consisted of a hollow metal cylinder (15 cm high, 11 cm diameter, closed at one end) which rested open-end-down on a small wooden platform (1.5 cm thick), which, in turn, rested directly on the ground. The cylinder restrained a mouse just before its release. A string was attached to the cylinder, and was threaded through a hole in a small wooden pole positioned directly above the metal cylinder. This string was then run parallel to the woodlot edge to a point 30 m from the cylinder. A tug on the string released the mouse by lifting the cylinder off of its wooden platform. Immediately after the lifting of the cylinder, the experimenter withdrew quietly and quickly from the area. We had no indication that any released mice detected the presence of the experimenter. However, to make this presence as neutral as possible, the experimenter was positioned at the same distance from the woods as the release mechanism, and always withdrew parallel to the edge of the woods in an easterly direction.

Tracking procedure

Mice were tracked using fluorescent tracking powder (Radiant Color Corp.). We used the technique described by Lemen and Freeman (1985), modified to prevent powder from coming in contact with a mouse's sensory organs (eyes, ears, and nose). The powdering procedure began by dropping a mouse into a plastic bag. The mouse was sheparded (head first) into a corner of the bag. A firm grip on the mouse was then obtained (through the bag) by carefully pinching the skin on the back of its neck. Once a secure hold was achieved, the bag was peeled back around the mouse until only its abdomen, rear legs, and back were exposed. The exposed portion of the mouse was coated completely with powder. The powdered mouse was then placed into the release mechanism, and released within a few minutes.

Mice were tracked the night after release. This was done using an ultraviolet lamp to illuminate the trail left by the powder as it fell off the mouse. Stick flags were placed in the ground along the trail at approximately one-meter intervals. Trails were followed until five min of searching revealed no additional powder. The next morning a compass and field tape were used to measure the bearing and distance from the point of release to (1) each flag, and (2) the nearest point along the woodlot edge.

Results

The white-footed mice released closest to the woodlot edge were most likely to succeed in reaching the woodlot (Table 1). However, the effect of release distance was only marginally significant (G -test, $\chi^2 = 5.05$, $P = 0.08$). It is possible that success in reaching the woodlot was underestimated, since our ability to track the mice

was not unlimited. We were sometimes able to track non-successful mice as far as 200 m, but on average (\pm SE) we could track unsuccessful 20-m and 30-m mice for $66.3 \pm (7.9)$ and $68.6 \pm (6.8)$ m respectively (10-m mice were usually successful at reaching the woods and were thus tracked only short distances). Since these tracking distances exceeded the minimum distance to the woodlot in all cases, our measure of success seems reasonable. It is, however, possible that these tracking distances were not sufficient to overcome any initial disorientation and trauma caused by the powdering and release procedures. We addressed this possibility with pilot work in which mice were released into a small brush pile rather than open ground. These "cover-released" mice were ultimately just as "lost" as open-released mice, even though the former clearly lingered (recuperated?) in the brush pile before heading out. We chose not to use cover-releases as they limited still further our ability to track mice (too much powder fell off a mouse before it left the brush pile).

A less stringent measure of success involved assessing whether mice were oriented towards the woodlot. Fig. 1 shows the angular orientation of mice at the point at which we lost the trail, or the point at which they entered the woodlot. There was a significant orientation towards the woodlot only for mice released at 10 m (V -test, $u = 2.68$, $P = 0.0039$; Batschelet 1981). Mice released at 20 m appeared oriented towards the woods to some degree, but the overall effect was only marginally significant (V -test, $u = 1.49$, $P = 0.07$). Mice released at 30 m were not significantly oriented towards the woods (V -test, $u = 1.16$, $P = 0.1314$).

There was no overall tendency for mice to be oriented towards their home woodlot for any treatment (Fig. 1; V -tests; 10-m mice, $u = 1.18$, $P = 0.126$; 20-m, mice $u = 0.06$, $P > 0.25$; 30 m mice, $u = 0.514$, $P > 0.25$). Overall, the mice were either oriented towards the woodlot or not oriented at all. There was also no significant difference in orientation between the sexes at 10 m (Mardia-Watson-Wheeler [MWW] test, $\chi^2 = 4.56$, $df = 2$, $P = 0.104$; female $n = 12$, male $n = 8$) or 20 m (MWW test, $\chi^2 = 1.10$, $df = 2$, $P = 0.604$; female $n = 10$, male $n = 10$), but there was a significant difference at 30 m (MWW test, $\chi^2 = 7.18$, $df = 2$, $P = 0.0286$; female $n = 10$, male $n = 9$). However, at 30 m, neither male (Rayleigh test, $rc = 0.138$, $P = 0.844$) nor female (Rayleigh test, $rc = 0.0048$, $P > 0.9$) mice showed significant orientation in any particular direction.

Table 1. Number of mice that were successful or unsuccessful in reaching the woodlot, as a function of release distance.

| | Release distance (m) | | |
|--------------|----------------------|----|----|
| | 10 | 20 | 30 |
| Successful | 14 | 10 | 7 |
| Unsuccessful | 6 | 10 | 13 |

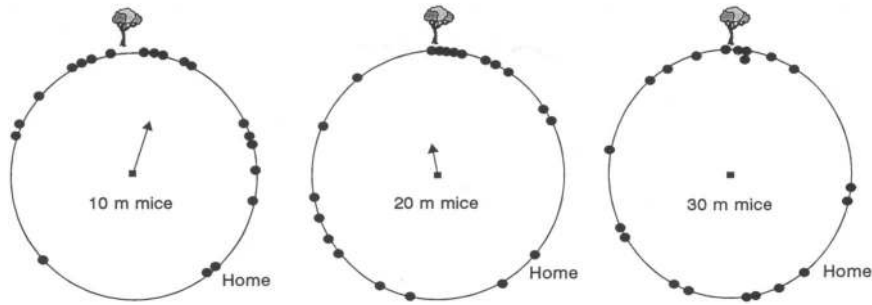


Fig. 1. Angular orientation of bare-field-released mice, defined relative to the point of release and the place at which the trail was lost, or where the trail entered the woodlot. Data are given for mice released at 10, 20, or 30 m from forest edge. The 20 dots on each unit circle represent the angular orientations of twenty individual mice, regardless of their actual displacement from the point of release. The tree symbol represents that part of the woodlot closest to the point of release (which was arbitrarily defined as 0° for each release). "Home" indicates the direction of the woodlot from which the mice were captured. The square at the center of each circle represents the point of release. Vectors indicate average angle and degree of orientation (or mean vectors, Batschelet 1981) for cases with statistically significant orientation (or near-significance, see text).

Discussion

Our results suggest that a mouse dispersing through an unfamiliar agricultural landscape may have considerable trouble locating forested habitat. White-footed mice were surprisingly unable to locate such habitat from a seemingly small distance away; the apparent perceptual range was about 20 m. One might argue that mice released at 30 m were aware of the woodlot but were less motivated to enter it than were mice released at shorter distances. We cannot rule out such a possibility, but it is difficult to explain why the 30-m mice would wish to linger in a barren field while 10-m and many 20-m mice headed straight for the woods. The most parsimonious interpretation is that the 30-m mice did not perceive the forest. We return to this point in a following section. The significantly different orientations between the sexes released at 30 m is curious considering that neither sex showed a significant orientation in any direction. Other studies also document no clear sexual differences in the navigational abilities of small mammals (Robinson and Falls 1965, Barry 1984).

The apparently limited navigational ability of white-footed mice in an unfamiliar landscape appears to contradict several studies demonstrating that *Peromyscus* mice may home successfully after being displaced up to 2–3 km from their home range (Teferi and Millar 1993 for a review). However, these studies demonstrate mainly that such mice can determine the direction home over considerable distances (perhaps via an ability to detect magnetic fields, August et al. 1989); the limited perceptual abilities indicated above suggest that white-footed mice would be unable to plan far ahead in determining the best path home.

Perceptual abilities in crop fields

Rationale

Fields of crops like soybeans represent a highly visually disruptive environment through which to disperse when compared to bare fields. Based upon the above results, we tested the hypothesis that a white-footed mouse's perceptual range drops to near zero in soybean fields. This potential effect of crop fields is not a trivial consideration in the midwestern USA, whose forest fragments are imbedded in a sea of crops for a large part of the year. The late summer–early autumn dispersal peak in white-footed mice (Krohne et al. 1984, Cummings and Vessey 1994) occurs when crops are in place, and thus mice dispersing at this time may be at a disadvantage in locating suitable habitat.

White-footed mice dispersing through crop fields might take advantage of resources and cover from predators that are unavailable in bare fields. These possible benefits of traveling in crop fields question our assumption that the perception of a woodlot is equivalent to behavioral action oriented towards it. Nevertheless, white-footed mice appear to perceive such fields as hostile places (Wegner and Merriam 1990). In the following section we describe trapping studies and behavioral experimentation which support further the validity of this assumption in soybean fields.

Our examination of the perceptual abilities of mice in soybean fields involved a two-part experiment. The first part involved the release of mice into a soybean field bordered by woods. This work was a straightforward extension of the bare field experiment. However, we also released "local" mice that were trapped in the forest immediately adjacent to the soybean field. These "local" releases were designed to address the assumption that soybean fields are hostile places for white-

footed mice. If mice at our study site were making voluntary forays into crop fields (cf. Merriam and Lanoue 1990, Cummings and Vessey 1994), then local (i.e. navigationally knowledgeable) mice should have been more adept at locating the woods than naive mice.

The second part involved the concurrent release of mice into a bare field. These releases determined whether the earlier bare-field results (obtained during the early spring) were relevant to the soybean field results (obtained during mid-summer). Additionally, soybean-released mice that were recaptured in the woods following their initial release were re-released. These re-releases determined whether "soybean" mice behaved similarly to bare-field mice when released under similar conditions.

Methods

The capture, handling, mechanics of release, and tracking of released mice were all done as described earlier. Here, we present methods specific to this experiment.

Study sites

All releases were done during July and August 1994 at two sites in western Indiana (Vigo County). The soybean release site was a level, 16-ha, rectangular field bordered to the east and south by second-growth hardwood forest (approximately 12 m in height) and to the west and north by roads and additional forest. Mice released at 10 and 30 m from the woods (see below) experienced forest horizon angles of 49 and 21°, respectively (assuming a visible 12-m forest). The soybean plants themselves were fully-grown (ca 75 cm high), with un-ripe fruit, and formed a completely closed canopy. These plants grew in rows that paralleled the edge of the woods on the eastern side of the field, along which all releases took place.

The bare-field release site was a level, 12.5-ha, oval-shaped field that was plowed just before experimentation, and it thus provided mice with a nearly vegetation-free environment similar to that in the earlier bare-field work. This bare field was bordered to the south, east and north by a floodplain hardwood forest (approximately 14 m in height) and to the west by a road and an additional field. Mice released at 10 and 30 m from the woods (see below) experienced forest horizon angles of 55 and 25°, respectively (assuming a visible 14-m forest).

Both release sites were 7 km southeast of the bare field site used in the earlier work. These two sites were also 0.5 km apart, separated by a road and a major stream (5 m in width). Non-local mice were all trapped at a site 7–8 km northwest of the two release sites.

Experimental design

Soybean releases followed a 2 × 2 factorial design involving local and non-local mice (mouse type) released

at two different distances from the forest edge (10 and 30 m). Ten mice were assigned randomly to a given distance-mouse-type combination. Local mice were trapped in the woods bordering the soybean field, all within 10–20 m of the field. These local mice were later released into the field immediately adjacent to their actual point of capture. Note that the orientational data were not analyzed using a two-way ANOVA-like technique of circular statistics. The problem here is that such techniques are still in their infancy (Fisher 1993). We thus used single-sample and pairwise tests (as per Batschelet 1981) in our analysis. This did not present any major problems in interpreting the results.

For the bare-field releases, "naive nonlocal" mice (not previously captured) were released at either 10 or 30 m from forest edge. Twelve mice were released at the 30-m distance, with only 5 released at the 10-m distance; this discrepancy reflected a shortage of mice, and the fact that the behavior of the 10-m mice was readily apparent from as few as 5 releases. Other bare-field releases involved recaptured soybean-released mice. We recaptured 13 such mice during routine trapping operations (see above) in the woods bordering the eastern edge of the soybean field (where all local mice were originally captured, and along which all mice were released). The first 10 recaptured mice were released only at the 10-m distance; we were unable to recapture enough mice for a more ambitious design.

Results

None of the 40 soybean-released mice were actually tracked to the forest. Our ability to track mice in soybean fields was limited relative to the spring bare-field experiments (average \pm S.E. tracking distances, $n = 10$ in all cases: 10 m, local: 24.1 m \pm 3.4; 10 m, nonlocal: 25.6 m \pm 3.8; 30 m, local: 33.0 m \pm 4.0; 30 m, nonlocal: 27.8 m \pm 3.7) but still usually sufficient for an oriented mouse to have reached the woods. Fig. 2 also shows that in no instance were the mice even oriented significantly towards the forest (V -tests, all $P_s \gg 0.15$; u -statistics – 10 m, non-local: $u = -1.71$, $P > 0.25$; 10 m, local: $u = -0.08$, $P > 0.25$; 30 m, non-local: $u = 0.02$, $P > 0.25$; 30 m, local, $u = 1.01$, $P = 0.1692$). Combining data across release distances (Fig. 3a), there was no difference in the orientation of local vs non-local mice (MWW test, $\chi^2 = 1.51$, $df = 2$, $P = 0.478$), nor were mice oriented towards the woods in either case (V -tests, all $P_s > 0.25$; u -statistics – non-local: $u = -1.14$, $P > 0.25$; local: $u = 0.47$, $P > 0.25$). Note also that non-local mice were not significantly oriented towards home (Fig. 3a; V -test, $u = 1.49$, $P = 0.0717$); the local mice were also not oriented towards home (the adjacent forest). Combining data across local and non-local mice reveals no tendency to be oriented towards the forest (Fig. 3b; V -tests, $P_s > 0.20$; u -statistics – 10 m: $u = -0.704$, $P > 0.25$; 30 m: $u = 0.78$, $P = 0.225$).

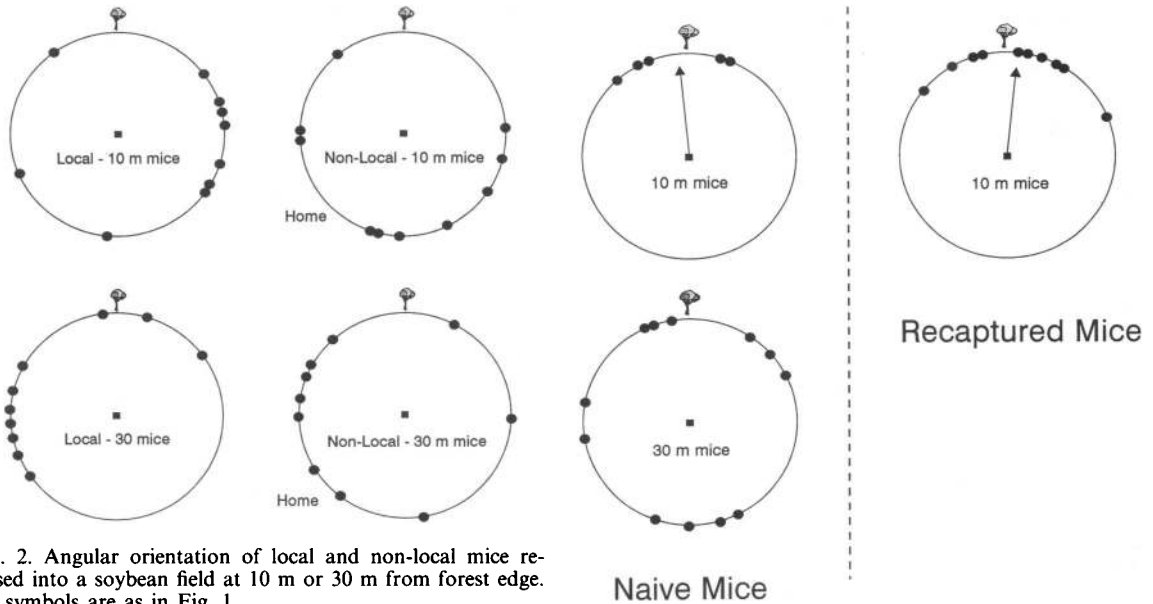


Fig. 2. Angular orientation of local and non-local mice released into a soybean field at 10 m or 30 m from forest edge. All symbols are as in Fig. 1.

There was, however, a significant difference between the orientation of 10 vs 30-m mice (MWW test, $\chi^2 = 9.85$, $df = 2$, $P = 0.0077$) due largely to a curious tendency for the 30-m mice to be oriented 270° (northward) relative to the forest edge (Rayleigh test, $rc = 0.377$, $P < 0.007$).

The bare-field releases yielded results similar to those seen earlier (Fig. 4). A significant orientation towards the forest was observed in both 10-m naive (V -test, $u = 2.80$, $P = 0.0009$) and 10-m re-captured mice (V -test, $u = 3.78$, $P < 0.0001$). In fact, all 10-m mice trav-

Fig. 4. Angular orientation of (a) "naive" mice released into a bare field at 10 m and 30 m from the forest edge, and (b) re-captured (soybean-released) mice re-released into a bare field at 10 m from forest edge. All symbols are as in Fig. 1.

eled directly to the forest. Only 33.3% (4 of 12) of the naive mice released at 30 m were actually tracked to the woods; this fraction was not significantly different from the 35.0% (7 of 20) success rate for mice in the earlier bare field experiment (G -test, $\chi^2 = 0.01$, $df = 1$, $P > 0.925$). The 30-m naive mice were also not significantly oriented towards the forest (V -test, $u = 0.30$, $P > 0.25$).

Were local soybean-released mice ultimately more likely to reach the forest than non-local mice? Several mice were recaptured in the bordering forest within 3 d of release. There were too few recaptures to make any definitive statements, but of the 13 recaptured mice, 8 were locals (6 from 10 m, 2 from 30 m) and 5 were non-local (4 from 10-m, 1 from 30-m). Regarding the effect of release distance, the number of recaptured 10-m and 30-m mice were 10 (6 local, 4 non-local) and 3 (2 local, 1 non-local), respectively. This difference between release distances was significant (G -test, $\chi^2 = 3.98$, $df = 1$, $P = 0.046$), whereas the difference between local and non-local mice was not significant (G -test, $\chi^2 = 0.70$, $df = 1$, $P > 0.442$).

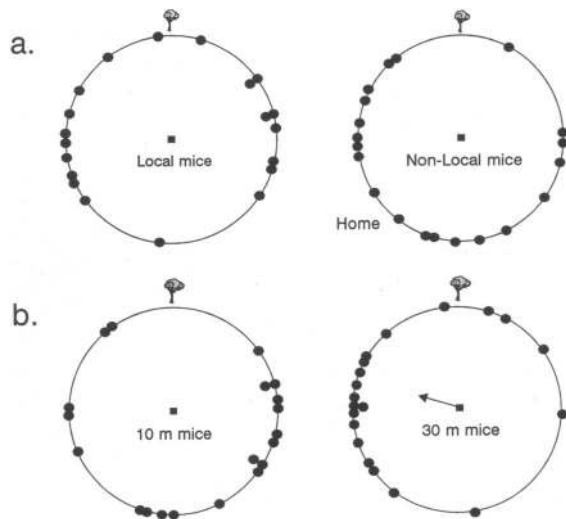


Fig. 3. (a) Angular orientation of soybean-released local and non-local mice, combining data across distance categories. (b) Angular orientation of soybean mice released at 10 m and 30 m, combining data across local and non-local categories. All symbols are as in Fig. 1.

Discussion

The results suggest a near-zero perceptual range for white-footed mice in soybean fields. For several reasons, we are confident that these mice would have oriented towards the forest had it been perceived (see also the following section). First, the bare-field releases of naive and recaptured individuals showed that these

mice were just as motivated in locating forested habitat as in the earlier bare-field work. Second, several mice (mainly 10-m releases) were eventually recaptured in the woods. Third, local mice appeared no more familiar with the soybean field than non-local mice, suggesting that they did not regularly enter this habitat.

Our results are consistent with the view that mice detect forested habitat primarily by vision. This is readily apparent when one considers an obvious auditory cue provided by katydids (Orthoptera). These forest-dwelling insects called constantly during every release night, and could easily have been used as a cue to locate forested habitat. Either mice cannot hear such sounds, or are unaware of the information they conveyed.

We cannot readily explain why mice appeared oriented in some circumstances (Fig. 3b). There was no indication that these mice were oriented towards home. The tendency of 30-m mice to orient on average parallel to the forest edge (Fig. 3b) may have reflected the orientation of crop rows. However, the paths of released mice were typically sinuous, and only rarely seemed influenced by the rows of soybean plants.

The critical assumption revisited

Rationale

As mentioned earlier, critical to our study is the assumption that the perception of a woodlot is equivalent to behavioral action oriented towards the woodlot. This is most easily justified in barren fields, in which a mouse's survival clearly means locating forested habitat. Such habitats not only lack food resources, but may also represent thermally stressful environments as well (e.g., Vispo and Bakken 1993). Furthermore, several studies demonstrate that many animals perceive a high risk of predation in exposed areas (Lima and Dill 1990). This appears to be a major reason why exposed areas are avoided by white-footed mice (Kaufman et al. 1983, Anderson 1986, Bowers and Dooley 1993).

The status of our critical assumption in soybean fields is not so obvious, as such habitats offer mice a potentially more benign environment. Several studies show that white-footed mice nonetheless avoid crop fields. In a study conducted near our study sites, Whitaker (1967a, b) found that white-footed mice are virtually absent from soybean fields. Recent studies in nearby eastern Illinois (Getz and Brightly 1986) and western Ohio (Williams et al. 1994) suggest a similar avoidance of crop fields. This general avoidance of agricultural fields by white-footed mice is also supported by other trapping studies (reviewed by Wegner and Merriam 1990; but see Cummings and Vessey 1994).

To assess further the validity of our critical assumption, we performed two additional studies. First, we performed trapping surveys in soybean and bare fields in the vicinity of our study sites to verify that white-footed mice avoid these habitats as we assumed. Second, we performed a habitat choice experiment in which mice were allowed to choose directly between forested and soybean habitats.

Methods

Trapping surveys

Trapping in agricultural habitats was conducted in large fields during the early spring (bare field) and late summer 1995 (soybean field). These two periods corresponded to the seasonal timing of the bare field and soybean field mouse-release experiments described earlier. Trapping was conducted at each site during two periods separated by 3–4 weeks.

Our trapping protocol in agricultural fields was based upon that of Whitaker (1967a, b). We placed 400 snap traps in a 20 × 20 square array with adjacent traps separated by 5 m. This array was aligned parallel to the edge of mature forest habitat, with traps placed from 10 m to 105 m from forest edge. Traps were set and baited with peanut butter during the 4 consecutive nights constituting a given trapping period. All traps were checked each morning.

Our trapping effort in woodlots involved Sherman live traps. These mice were being trapped for experimental purposes unrelated to the present study. (Note that all captured mice were released well beyond their ability to return to their home woodlot.) Sherman live traps are generally not as effective as snap traps in capturing mice (J. O. Whitaker, pers. comm., and P. Zollner, pers. obs.), and thus their use in woodlots provided a conservative estimate of the difference between forest and field habitats. Live traps were placed in the same density used in agricultural fields, but in smaller numbers (usually 75–150 traps per night). We report woodlot trapping results obtained contemporaneously with the field trapping results to which they were to be compared. We trapped mice from two different forest sites separated by over 10 km. Neither site was closer than 4 km to an agricultural trapping site.

Habitat choice experiment

Mice were given a choice between entering forested habitat or soybean habitat upon being released into a small, vegetation-free area between the two. There were 5 such release sites, each of which measured 8 × 20 m; the long axis paralleled the forest, thus 8 m separated soybean and forested habitats. The short sides of the release sites (sides perpendicular to the forest edge) were bordered mainly by grasses approximately 60 cm in height.

Mice were released at one of three locations in a given site: 1, 4, or 7 m from the forest edge (or, respectively, 7, 4, and 1 m from the soybean edge). Ten mice were released in random order at each location. Mice were handled, released, and tracked as per the previously described experiments. The single methodological change involved a modified release mechanism which provided mice with a view of both habitats before their actual release. This modification reflected our goal that the mice be allowed to essentially choose habitats before their release; with the release mechanism so close (e.g., 1 m) to one habitat or another, the results could have been influenced by the direction chosen by a mouse during its haphazard dash out from the opaque holding cylinder used previously. The new holding cylinder (17 cm high, 23 cm diameter) was constructed from wire-mesh (1.27 cm² mesh size) and capped with a solid metal roof. One side (180°) of the cylinder was covered with opaque tape, which obstructed a mouse's view of the experimenter prior to release. The unobstructed side of the release mechanism was oriented such that the mouse had an equally clear view of both habitats. Each mouse was held in this cylinder for 5 min before release.

Results

Trapping surveys

White-footed mice were vastly more abundant in forested habitat than in agricultural fields (Table 2). The capture rate in forested habitat was 42 times higher than the overall bare-field capture rate of 0.031 mice per 100 trap nights. Quantitatively very similar results were obtained in the comparison between forested and soybean habitats. The capture rate in forested habitat exceeded the overall capture rate in soybean fields (0.125 mice per 100 trap nights) by a factor of 23.

Habitat choice experiment

Twenty-six of the 30 released mice were tracked directly to the forested habitat (Table 3). This overall preference for forested over soybean habitats is highly significant

Table 2. Results from trapping surveys of white-footed mouse abundance in agricultural fields vs forest habitat.

| | Mice captured | Trap nights | Captures per 100 trap nights |
|----------------------------|---------------|-------------|------------------------------|
| a. Bare field vs forest | | | |
| bare field, period 1 | 0 | 1600 | 0 |
| bare field, period 2 | 1 | 1600 | 0.056 |
| forest | 50 | 3778 | 1.32 |
| b. Soybean field vs forest | | | |
| soybean, period 1 | 1 | 1600 | 0.056 |
| soybean, period 2 | 3 | 1600 | 0.188 |
| forest | 36 | 1264 | 2.85 |

Table 3. Number of mice choosing forest or soybean habitats as a function of release distance from forest.

| | Release distance (m) | | |
|----------|----------------------|---|---|
| | 1 | 4 | 7 |
| Forest | 8 | 9 | 9 |
| Soybeans | 2 | 1 | 1 |

(*G*-test, $\chi^2 = 18.0$, *df* = 2, *P* < 0.001). There were too few mice tracked into the soybeans to discern any effect of release distance, but it is clear that even mice released only 1 m from soybeans (or 7 m from the forest) still strongly preferred to travel to the more distant forest (Table 3).

Discussion

The general avoidance of agricultural habitats by white-footed mice provides support for our assumption that soybean and bare fields are hostile habitats in which the perception of forested habitat would be equivalent to behavioral action oriented towards it. Our trapping results are in accord with several earlier studies showing an avoidance of agricultural fields (Wegner and Merriam 1990), and in excellent quantitative agreement with trapping surveys performed earlier in the vicinity of our study sites (Whitaker 1967a, b). We cannot readily explain, however, why a few mice ran straight into the soybeans upon their release during the habitat choice experiment (Table 3).

General discussion

An understanding of key behavioral attributes of animals inhabiting a given landscape may provide much insight into landscape-level ecological processes (Hansson 1991, Merriam 1991, Dunning et al. 1992, 1995, Wiens et al. 1993, Gross et al. 1995, Lima and Zollner 1996). Here, we have explored one of these attributes, perceptual range, which we believe to be an important determinant of a variety of landscape-level ecological phenomena (Lima and Zollner 1996).

Our experimental work on the perceptual range of white-footed mice suggests that they have a surprisingly limited perceptual range. This was the case not only in a visually obstructive environment like crop fields, but also in bare fields with no such obstructions. White-footed mice thus appear rather disadvantaged in locating fragmented forested habitat within an agricultural landscape.

Further empirical determinations of perceptual range will likely show a large range of perceptual abilities among animals. We fully expect that some species (especially birds) possess such great perceptual ranges

that they may choose among habitat patches that can be viewed simultaneously from a remote location, while other species must literally bump into suitable habitat before discovering it. Such differences should reinforce the idea that the ecological effects of a given landscape configuration will be determined in part by the behavioral attributes of the species in question.

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