ANIMAL BEHAVIOUR, 1999, **58**, 489–500
Article No. anbe.1999.1186, available online at http://www.idealibrary.com on IDEAL

Illumination and the perception of remote habitat patches by white-footed mice

PATRICK A. ZOLLNER & STEVEN L. LIMA
Department of Life Sciences, Indiana State University

(Received 3 August 1998; initial acceptance 13 December 1998; final acceptance 10 May 1999; MS. number: A8270)

Perceptual range, or the distance at which habitat 'patches' can be perceived, constrains an animal's informational window on a given landscape. If such constraints are great, they may limit successful dispersal between distant habitat patches. On dark nights, nocturnal white-footed mice, *Peromyscus leucopus*, have surprisingly limited perceptual abilities regarding distant forested habitat. In fact, their ability to orient towards such habitat while travelling in a bare agricultural field indicates a perceptual range under 30 m. However, increasing illumination can increase perceptual range. For example, full moonlight extends the perceptual range of mice to about 60 m. Light levels at dusk (twilight) extend perceptual range still further to about 90 m. These results suggest that interpatch dispersal by white-footed mice would be more successful under greater illumination, but travelling under such conditions entails a considerable risk of predation. These mice might avoid such a conflict by travelling under the cover of darkness with the aid of information gathered remotely during relatively high illumination. We show that mice are indeed capable of such a 'look now and move later' strategy: mice retain directional information gained under bright conditions and maintain a previously determined bearing in conditions under which distant navigational stimuli may be largely absent (e.g. maximal darkness). Ultimately, a better understanding of the behavioural and ecological factors affecting the movements of animals across landscapes should produce a clearer picture of the interaction between landscape structure and population ecology.

Empirical information on 'landscape-level' behavioural phenomena is an important missing link in the study of animal ecology at large spatial scales (Stamps et al. 1987; Wiens et al. 1993; Kareiva & Wennergren 1995; Lima & Zollner 1996; but see Ruckelshaus et al. 1997). In particular, the development of spatially explicit population models (Dunning et al. 1995) may be limited by an inadequate understanding of the behavioural mechanisms underlying dispersal and habitat selection (Wennergren et al. 1995). It is clear that until we develop a better understanding of such mechanisms and the information available to animals at the landscape level, models of this sort are unlikely to achieve their full potential (Lima & Zollner 1996).

The phenomenon of perceptual range, or the maximum distance from which an animal can perceive landscape elements, illustrates the important role that behaviour can play in landscape-level processes (Zollner & Lima 1997). For example, an animal's perceptual range should influence both its choice of search strategy during dispersal and its probability of successfully reaching a new patch (Zollner & Lima 1999). Perceptual range is thus an important determinant of landscape connectivity (Lima & Zollner 1996) and population dynamics in fragmented landscapes (see also Fahrig 1988; Pulliam et al. 1992; Turner et al. 1994). Surprisingly, there is remarkably little empirical information on the perceptual range of vertebrates. Presently, we know only that an aquatic turtle, the yellow-bellied pond slider, *Trachemys scripta*, is able to perceive bodies of water from at least 300 m away (Yeomans 1995), that red-backed voles, *Clethrionomys gapperi*, can perceive forested habitat from approximately 10 m away (Gillis & Nams 1998), and that white-footed mice, *Peromyscus leucopus*, are able to perceive forested habitat from no further than 30 m on dark nights (Zollner & Lima 1997).

We also know little about the way in which perceptual range varies with ecological circumstances. Nevertheless, perceptual range is likely to be influenced by a variety of factors. For example, displaced pond sliders locate nearby ponds from much greater distances on days when the sky

Correspondence and present address: P. A. Zollner, USDA Forest Service, North Central Research Station, 5985 Highway K, Rhinelander, WI 54501-9128, U.S.A. (email: pzollner@newnorth.net). S. L. Lima is at the Department of Life Sciences, Indiana State University, Terre Haute, IN 47809, U.S.A.

is clear than on cloudy days (Yeomans 1995). Similarly, the spatial navigational abilities of meadow voles, *Microtus pennsylvanicus*, in water mazes are diminished on overcast days (Kavaliers & Galea 1994). Some animals may also use cues from conspecifics or other species to perceive distant habitat, which may reduce recruitment to uninhabited patches (Smith & Peacock 1990; Reed & Dobson 1993). Thus perceptual range is not likely to be a fixed entity as is frequently assumed in population models (e.g. Pulliam et al. 1992; Turner et al. 1993; Liu et al. 1995; Schippers et al. 1996).

For nocturnal animals, ambient illumination is likely to be a strong determinant of perceptual range. Our previous work on white-footed mice indicates that on dark nights these mice cannot detect woods from beyond 30 m while travelling in bare fields, or from even 10 m while in fields with mature (visually obstructive) crops (Zollner & Lima 1997). This suggests that white-footed mice use vision to detect forested habitat. Mice of the genus *Peromyscus* are known to have considerable visual acuity for small rodents (King 1968; King & Vestal 1974), and can better distinguish between objects as illumination levels increase (Barry 1984). Additionally, these mice appear to use nearby visual landmarks while navigating in laboratory situations (Joslin 1977; Barry & Franq 1982) and natural habitat (Barry & Franq 1980; Drickamer & Stuart 1984). If vision is indeed the mechanism by which white-footed mice detect remote landscape elements, then their perceptual abilities should increase as ambient illumination increases.

Thus our goal was to examine how the perceptual range of white-footed mice is influenced by ambient illumination. In the following sections, we present our general methodology and describe two experiments examining the influence of illumination on perceptual range. The first experiment compared the perceptual range of white-footed mice during dark and moonlit nights. The second experiment addressed perceptual range under twilight conditions and the ability of mice to use 'twilight information' when travelling after dark. These experiments demonstrate that the perceptual abilities of white-footed mice, while limited, are strongly influenced by ambient illumination, and that mice are capable of retaining orientational information gained remotely during bright conditions for travel during dark (safe) conditions.

GENERAL METHODS

Ecological model systems (EMS) provide a method to examine, at a logistically feasible scale, mechanisms that have important implications for processes at larger ecological scales (Wiens et al. 1993). We used an EMS to simulate dispersal by white-footed mice searching for forested habitat in an unfamiliar agricultural landscape. We captured white-footed mice at remote locations and moved them several kilometres to a bare, fallow field. The mice were then released at various distances from the edge of a mature woodlot. The tendency of these mice to orient towards the woodlot was used to estimate the extent of their ability to perceive distant forested habitat. This translocation protocol for determining perceptual range was based on the assumption that the perception of the woods is equivalent to orientation towards the woods. This is a reasonable assumption, because bare, fallow fields are unsuitable places for white-footed mice; if mice perceive forested habitat they should attempt to reach it (see also Zollner & Lima 1997). Furthermore, habitat choice experiments and trapping surveys demonstrate that white-footed mice strongly avoid bare fields (Zollner & Lima 1997). Results discussed below also bolster the assumption that perception of the woods equals orientation towards the woods.

Study Site

The primary study site was in west-central Indiana (Vermillion County). White-footed mice were released at this site from March to May 1995 (spring releases) and from September to November 1995 (autumn releases). This study site was a level, 50-ha, rectangular agricultural field bordered immediately to the east by a 4-ha hardwood forest. This forest woodlot was approximately 15 m in height, thus mice released 10, 30, 60 and 90 m away from it (see below) faced respective forest horizon angles of 56, 27, 14 and 10°. To the west was additional forest, no closer than 500 m from the nearest release site. The southern and northern edges of the field were bordered by paved roads, beyond which were additional agricultural fields. This field had been planted in soybeans prior to each release period, and was devoid of vegetative cover at the time of releases.

Capture and Handling

We used Sherman live traps to capture white-footed mice in mature woodlots that were at least 5 km away from the release site. This 5-km minimum distance, and the barriers to movement (roads, streams, etc.) between capture and release sites, minimized the chance that captured mice had prior experience at the study site (Cooke & Terman 1977; Teferi & Millar 1993). Captured white-footed mice were housed in their traps in a small, unheated shed during the daylight period prior to their release. We provisioned each mouse with black oil sunflower seeds to sustain it until release. At the time of release, mice were transported to the study site and placed (individually) in release mechanisms under the appropriate conditions (see below).

We used only adult mice in these experiments. We distinguished white-footed mice from deer mice, *P. maniculatus bairdii*, as per Whitaker (1982), and all pregnant or lactating mice were excluded from the experiments (released at point of capture). Both male and female white-footed mice were used, as previous work with this translocation protocol indicated that the sexes do not differ in their ability to perceive distant habitat (Zollner & Lima 1997). This is consistent with the observation that sex does not influence the abilities of deer mice to detect visual stimuli in Morris water-maze tasks (Kavaliers et al. 1996).

Release

Releases were accomplished using a standard 'release mechanism', which provided mice with a view of the woods before their actual release. A holding cylinder (17 cm high, 23 cm diameter) was constructed from wire mesh ('hardware cloth' with mesh size of 1.27 cm^2) and capped with a solid metal roof. This cylinder rested on a wooden platform (25 × 25 cm and 2 cm thick). One side (180°) of the cylinder was covered with an opaque material that obstructed a mouse's view of the experimenter prior to release. The unobstructed side of the release mechanism was oriented such that a mouse had an equally clear view of the woods (to the east) and the bare field (to the west). The actual release locations were spaced uniformly along the edge of the woods, and there was no other woody vegetation within 300 m of any release location. The 600-m long edge of the woods allowed release sites to be spaced such that no animals were released within 50 m of each other on any given night. No new mice were released at a given location until rain had removed all traces of tracking powder from previous releases (see below). Such rainfall should have also minimized or removed any potential olfactory cues left by previously released mice. The release itself was accomplished by pulling on a string, which lifted the release mechanism off of its wooden platform (Zollner & Lima 1997). This was done from a distance of 60 m away from the release mechanism, with the string positioned parallel to the edge of the woods. Immediately following release the experimenter quietly left the release site along a line parallel to the edge of the woods. Thus, any effect of the experimenter's presence should not have biased mice to move towards or away from the woods.

Across all experiments, mice were held in the release mechanism for a standardized period based on the holding period that would have been used in the twilight information experiment (see below) on that day. Overall, holding times varied from 25 to 65 min using this procedure, depending upon the overall duration of the sunset and cloud cover in the sky. Note that all experiments were conducted concurrently at the same study site during the same field season, so there were no biases in holding time between experiments or treatments (release distances). We assigned captured mice to a given experiment according to a systematic schedule. This schedule rotated through experiments sequentially (one mouse per experiment per rotation), and was dependent upon the moon's phase for certain experiments (see below). Within an experiment, mice were assigned randomly to treatments.

Tracking Procedure

Mice were tracked using fluorescent tracking powder (Radiant Color Corp., Richmond, California), according to the technique described by Lemen & Freeman (1985). We modified this technique to prevent powder from coming in contact with a mouse's sensory organs (eyes, ears and nose; Zollner & Lima 1997). The night after release, the trail of powder left by a mouse was followed using an ultraviolet lamp. Stick flags were placed in the ground along each trail at approximately 1-m intervals. Trails were followed until they reached the woods or until they were so faint that 5 min of searching revealed no additional powder. During daylight, we used a compass and field tape to measure the bearing and distance from the point of release to (1) each flag in the trail and (2) the nearest point along the woodlot edge. All trails that did not reach the woods were at least 30 m long and most exceeded 50 m in length.

Analysis

We assessed perceptual abilities (in part) by determining whether mice were oriented towards the woods. We analysed the angular orientations of each mouse's initial movement out of the release mechanism (after travelling 1 m) for orientation towards the woods using V tests (Batschelet 1981). We analysed initial orientations rather than final orientations (Zollner & Lima 1997) to ensure that mice were not oriented towards the woods as an artefact of random wanderings (Goodwin et al. 1999). Additionally, the locations of mice after each had travelled 10 m, were tested against a random expectation (relative to the point of release) using Hotelling's one-sample test (Batschelet 1981). Significance under this test indicates that the distributional centre of these 10-m locations was significantly displaced away from the point of release. This test thus confirmed whether the mice remained oriented in the same direction as they moved away from the point of release. To assess whether mice were oriented towards their home wood, we analysed the angular orientations of the last point to which each mouse was tracked relative to the homeward direction (site of capture) using V tests. We also examined the possibility of seasonal (spring versus autumn) effects on initial orientations with Mardia–Watson–Wheeler pairwise tests, and on location after 10 m with Hotelling's two-sample test (following Batschelet 1981). All such tests failed to demonstrate any seasonal differences in orientation (Mardia–Watson–Wheeler tests: χ^2_2 range 0.04–3.28, P 0.98–0.19; Hotelling's two sample tests: N=20, T range 0.55–2.81, P range 0.75–0.31), hence spring and autumn data were combined before conducting the above statistical tests.

MOONLIGHT AND PERCEPTUAL ABILITIES

This section examines the hypothesis that white-footed mice have a greater perceptual range during periods of bright moonlight than under moonless or cloudy nocturnal conditions. White-footed mice may be active during bright portions of the night (Barry & Franq 1982), and they are better at differentiating among simple, nearby objects in simulated full moonlight than under moonless conditions (Barry 1984). In experiments where mice in the genus *Peromyscus* were given control of illumination, they selected conditions that were somewhat brighter than those on a moonless night (King 1975; Kavanau & Havenhill 1975). Other laboratory work has

demonstrated that *Peromyscus* orient towards an artificial moon, possibly using it as a navigational aid (Kavanau 1968, 1969). It thus seems reasonable to hypothesize that the long-range perceptual abilities of white-footed mice would be greater with bright moonlight than on dark nights.

Methods

For dark night treatments, mice were released at least 1 h after the onset of darkness (defined as the time when scattered light from the sun was less than that from starlight and other natural sources) on moonless nights or nights with heavy overcast. Releases were done at 10 or 30 m from the edge of the woods. Ten mice were released at each distance during each season (spring and autumn). These releases effectively replicated earlier research from another site (Zollner & Lima 1997), and determined whether our previous dark night results still applied at this new site.

For bright moonlight treatments, mice were released at least 1 h after darkness under a mostly cloud-free sky with a half to full moon positioned at least 45° above the horizon. Under these conditions mice were released at 30, 60 and 90 m from the edge of the woods. These distances were chosen based upon pilot work. As before, 10 mice were released at each distance during each season (spring and autumn).

The lunar cycle complicated the timing of releases. First, within a night, the limited time period with appropriate moonlight conditions (moon 45° above horizon) necessitated that all mice be released before 0300 hours (ensuring at least 2.5 h of movement before dawn). Mice released under dark night conditions were generally released before midnight. Second, because nearly full moons were only available for a portion of each lunar cycle, bright moonlight releases were temporally clumped around full moons, just as dark night releases were temporally clumped around new moons. Any biases associated with this temporal clumping should be minimal as each experiment covered several lunar cycles.

Results and Discussion

The perceptual abilities of white-footed mice released on dark nights were similar to those observed during previous work (Zollner & Lima 1997), despite the methodological changes (different holding mechanism, holding times and release site) employed in the present experiments. As before, mice were orientated towards the woods from 10 m but not from 30 m (Fig. 1). Mice released at 10 m were initially orientated towards the woods (V test: U=3.17, N=20, P=0.001), and after 10 m of movement, their average location was significantly displaced away from the point of release (Hotelling's one-way test: T^2=8.76, N=20, P=0.035). In contrast, mice released at 30 m were not initially orientated towards the woods (V test: U=0.89, N=20, NS) nor was their average location significantly displaced away from the point of release after moving 10 m (Hotelling's one-way test: T^2=0.69, N=20, NS). Mice not significantly orientated towards the woods were also not orientated in a homeward direction (at 30 m: V test, U= − 0.16, N=20, NS), in agreement with patterns documented previously (Zollner & Lima 1997).

Perceptual abilities were greater for white-footed mice released during full moonlight (Fig. 2) than for those released during maximum darkness (Fig. 1). With bright moonlight, mice released at both 30 and 60 m were initially orientated towards the woods (V tests: at 30 m: U=2.29, N=20, P=0.015; at 60 m: U=2.29, N=20, P=0.015) and after 10 m of travel, the average location of these mice was significantly displaced away from the point of release (Hotelling's one-way tests: at 30 m: T^2=11.96, N=20, P=0.014; at 60 m: T^2=11.99, N=20, P=0.013). Mice released at 90 m under moonlit conditions (Fig. 2) were not initially orientated towards the woods (V test: U=1.17, N=20, NS) and their average location after moving 10 m was not significantly displaced from the point of release (Hotelling's one-way test: T^2=1.31, N=20, NS). Finally, mice not significantly orientated towards the woods also failed to show a significant orientation towards home (V test: at 90 m: U=1.28, N=20, NS).

Our orientation data (Figs 1, 2) suggest that the mice may have initially moved in a direction that was intermediate between the woods and the site where they were captured (home). Perhaps this movement reflected a trade-off between the benefits of moving through cover and moving straight towards home (Cooke & Terman 1977; Teferi & Millar 1993). However, our analysis did not indicate any significant homeward tendency, even for those mice that were not significantly orientated towards the woods (see above). Experiments discussed below suggest that the 'intermediate' orientation noted above results from mice preferentially moving away from the occluded side of the release mechanism towards the portion of the field they had been viewing previously.

White-footed mice clearly have greater perceptual abilities under brighter conditions, but they are not necessarily likely to disperse during full moonlight. Several studies demonstrate that nocturnal rodents in general (Kotler 1984; Brown et al. 1988; Bowers 1990; Longland & Price 1991; Vásquez 1994, 1996), including *Peromyscus* mice (Clarke 1983; Travers et al. 1988; Wolfe & Summerlin 1989; Brillhart & Kaufman 1991; Clarke & Kaufman 1991; Bowers & Dooley 1993; Jekanoski & Kaufman 1995; but see Barry & Franq 1982) decrease levels of activity under bright moonlight. *Peromyscus* mice also increase their use of cover under bright moonlight (Clarke 1983; Travers et al. 1988; Wolfe & Summerlin 1989; but see McMillian & Kaufman 1994). Evidence strongly suggests that these behavioural responses to bright light are in response to a heightened risk of predation (Clarke 1983; Kotler et al. 1991, 1992; see Lima 1998 for a review). All of this implies that nocturnal dispersal would be relatively risky under bright conditions.

These results suggest that a trade-off between perceptual abilities and predation risk may influence a mouse's decision about when to disperse. The greater perceptual abilities associated with bright moonlight may

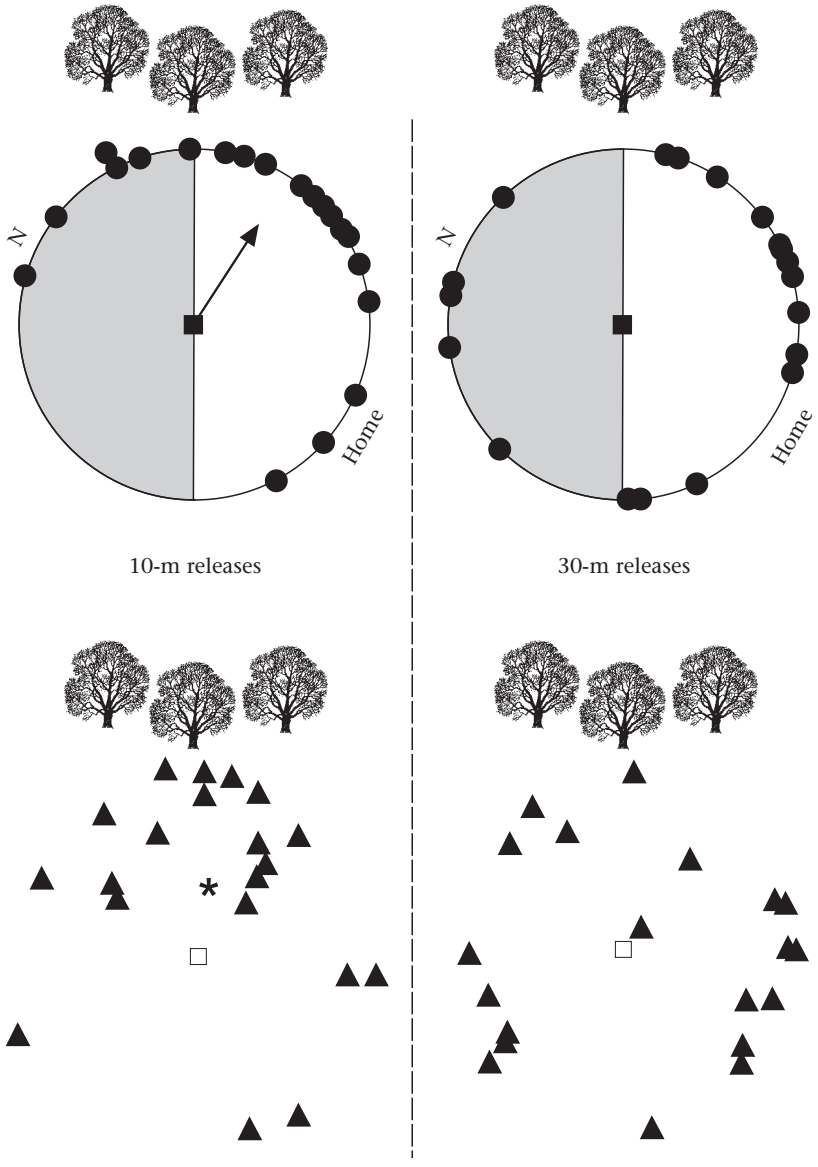

Figure 1. Initial orientation and movement of white-footed mice released on dark nights. The upper panel depicts the angular orientation of mice (circles), relative to the point of release (square), after 1 m of movement. Results are shown for each mouse released at 10 and 30 m from the forest edge. The tree symbols represent the direction of the shortest distance between the woodlot and the point of release. Vectors indicate average angle and degree of orientation (or mean vectors; Batschelet 1981) only for cases with statistically significant orientation towards the woods. 'Home' indicates the average direction to the point at which the mice were captured. 'N' indicates the average direction to cardinal north. True home and north were within 30° of the bearings indicated. The shaded portion of each circle reflects the orientation of that portion of the release mechanism occluded by an opaque cover. The lower panel depicts the exact location of each mouse after it travelled 10 m (triangles) regardless of its actual displacement from the point of release. The open square represents the location of the release mechanism. An asterisk indicates the average location of all mice after 10 m of movement; asterisks are shown only when the displacement of mice away from the point of release differed significantly from random.

significantly reduce searching time and thus the time exposed to predators while dispersing. However, mice moving under bright conditions are more easily detected by predators. The optimal trade-off depends on the overall risk of predation, energy reserves and realized perceptual ranges (unpublished data). A similar trade-off between perceptual range and risk has been suggested for *Anolis* lizards: juvenile lizards can climb trees to increase their ability to view a patch, but in doing so they face a greater risk of predation (Stamps 1991).

TWILIGHT INFORMATION AND PERCEPTUAL RANGE

In this section we focus on two related issues. First, we address the expectation that white-footed mice have greater perceptual abilities at twilight (dusk) than at night under moonlit conditions (which are considerably darker than at dusk). White-footed mice are primarily nocturnal, but they may be active before darkness and thus in a position to assess their landscape. In fact, it has been

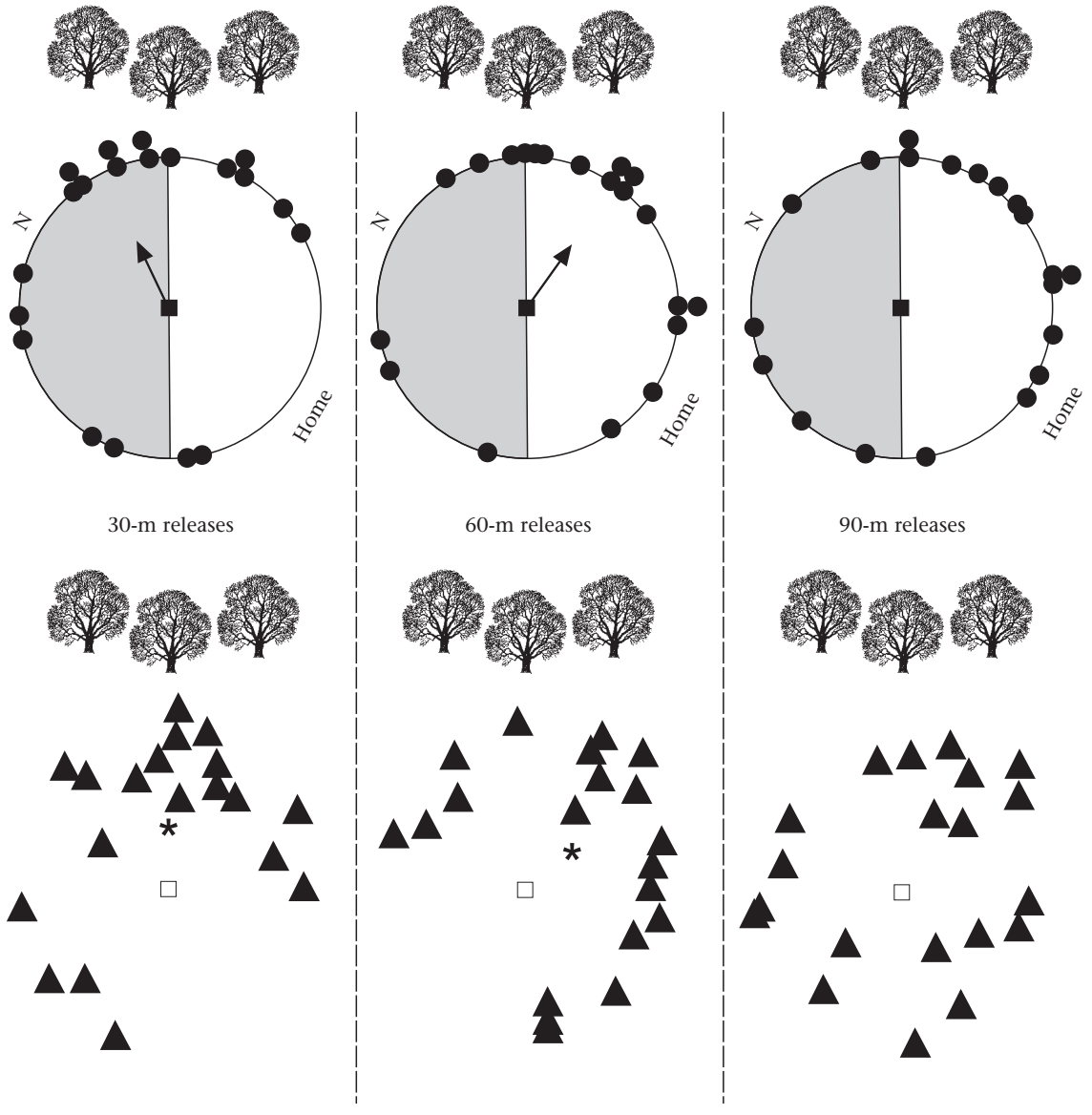

Figure 2. Initial orientation and movement of white-footed mice released during bright moonlight. Results are shown for mice released at 30, 60 and 90 m from the forest edge. The upper panel depicts the angular orientation of individual mice, relative to the point of release, after 1 m of movement. The lower panel depicts the exact location of each mouse after it travelled 10 m regardless of its actual displacement from the point of release. All symbols are as in Fig. 1.

suggested that *Peromyscus* activity peaks at dusk (Svihla 1932; Burt 1940), and deer mice show maximum activity in the laboratory when light levels are equivalent to late dusk or early dawn (Kavanau 1967). However, mice dispersing at twilight presumably face even higher predation risk than they would face if moving during bright moonlight. Dispersers might avoid much of this increased risk by gathering information at twilight and waiting to disperse under the cover of darkness. Thus our second focus was to examine whether these mice can use a 'look now and move later' strategy, in which they must (1) retain directional information gained earlier in the day and (2) maintain a previously determined bearing in conditions under which distant navigational stimuli may be largely absent (e.g. maximal darkness). Anecdotal evidence suggests that white-footed mice may use just such a tactic. Sheppe (1965) documented natural dispersal by white-footed mice between islands as far apart as 125 m. These movements were unlikely to have occurred during daylight conditions, and Sheppe (1965) surmised that mice might detect islands during daylight and move (swim) between them after dark.

To examine perceptual range at twilight and the possible use of 'twilight information' in night-time navigation, we released white-footed mice under maximal darkness after they were allowed to view their surroundings at twilight. If these mice have a relatively great perceptual range at dusk and can use twilight information while travelling after dark, then their ability to orient towards a wood should exceed that of 'uninformed' mice released on dark or moonlit nights.

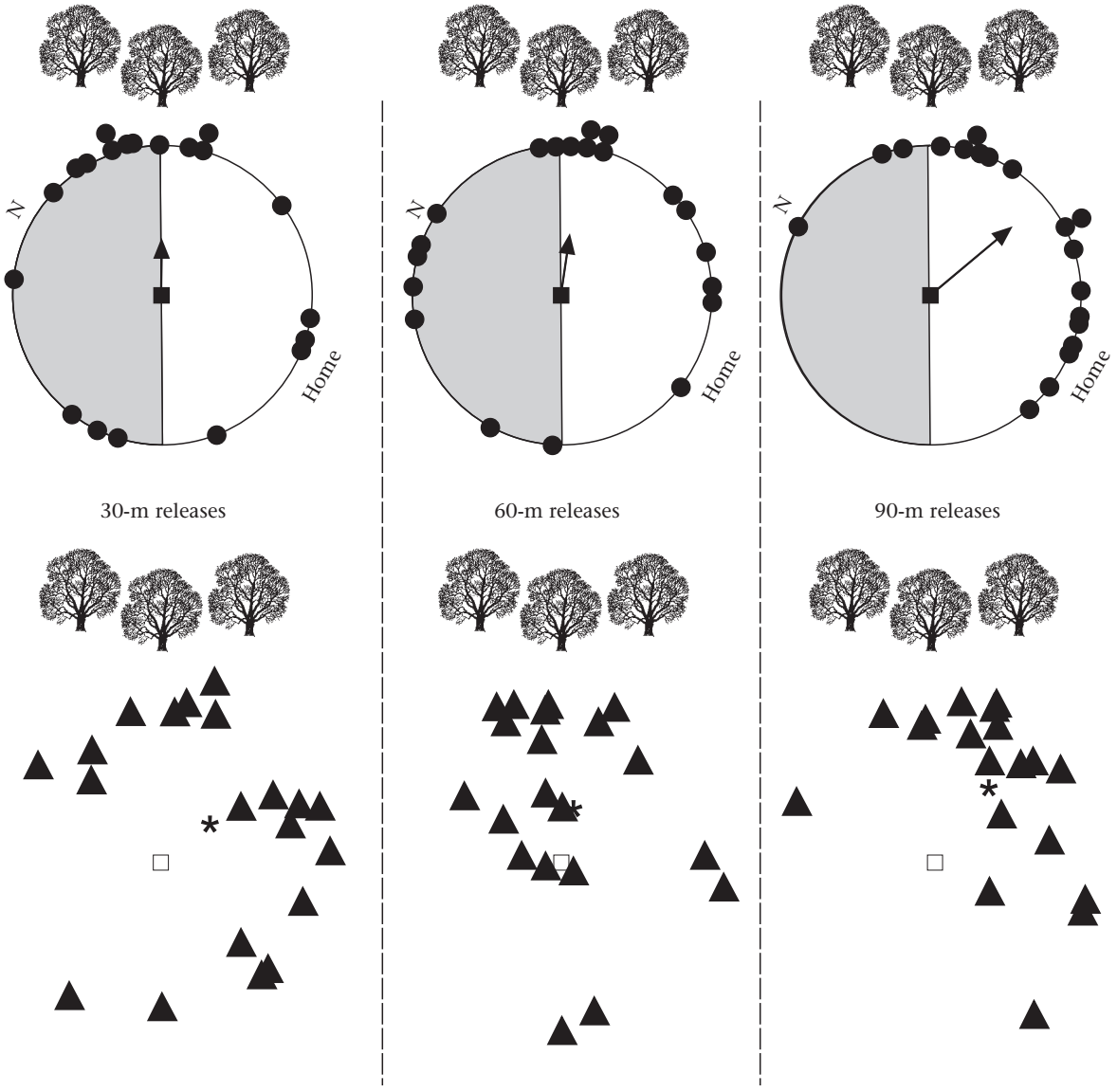

Figure 3. Initial orientation and movement of white-footed mice released during dark nights after a twilight view of the forest. Results are shown for mice released at 30, 60 and 90 m from the forest edge. The upper panel depicts the angular orientation of individual mice, relative to the point of release, after 1 m of movement. The lower panel depicts the exact location of each mouse after it travelled 10 m regardless of its actual displacement from the point of release. All symbols are as in Fig. 1.

Methods

Twilight-informed releases were performed only on dark nights (as above). Mice were placed in the standard release mechanism at the onset of twilight (defined as the beginning of civil twilight; Mitton 1991) and held until darkness (see above). In practice, the length of this holding period varied from 25 to 65 min (average 45 min). Mice were released at 30, 60 and 90 m from the edge of the woods. As before, 10 mice were released at each of the three distances during each season (spring and autumn).

Following the above releases, it was clear that further work was needed to define the outer limits of the perceptual abilities of these twilight-informed mice. Thus an additional experiment was conducted during April and May of 1996. During this experiment, 20 mice were released at both 60 and 120 m from the woods. These releases were conducted at a field in Vigo County, Indiana, which had been used in earlier work on the perceptual abilities of white-footed mice (Zollner & Lima 1997). The change of field sites was made necessary by logistical difficulties and changes in crop rotations at the primary study site. The trees were slightly taller at this secondary site (16 m instead of 15 m), but otherwise the two fields were very similar.

Results and Discussion

The results from the first set of releases (at the primary study site) clearly suggest that the perceptual range of white-footed mice at dusk exceeds 90 m (Fig. 3). These

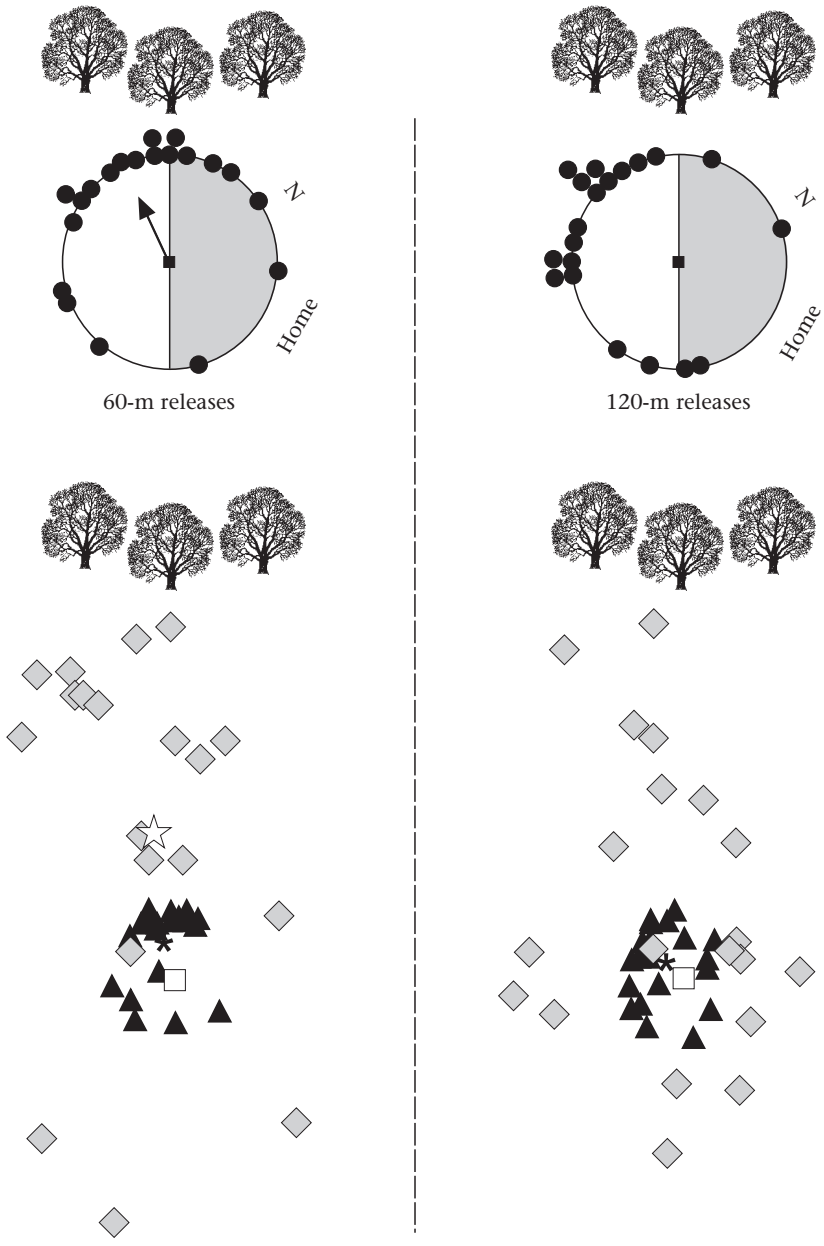

Figure 4. Initial orientation and movement of white-footed mice released at the secondary site during dark nights after a twilight view of the forest. Results are shown for mice released at 60 and 120 m from the forest edge. The upper panel depicts the angular orientation of individual mice, relative to the point of release, after 1 m of movement. The lower panel depicts the exact location of each mouse after it travelled 10 m (triangles) and 60 m (shaded diamonds) regardless of its actual displacement from the point of release. The average locations after travelling 10 m (asterisks) and 60 m (stars) are shown only when mice were significantly displaced from the point of release. All other symbols are as in Fig. 1.

results demonstrated that the initial movements of all twilight-informed mice were significantly orientated towards the woods (*V* tests: at 30 m: U=2.07, N=20, P=0.027; at 60 m: U=2.26, N=20, P=0.016; at 90 m: U=2.43, N=20, P=0.009), and that the average location after moving 10 m was significantly displaced from the point of release (Hotelling's one-way tests: at 30 m: T^2=8.91, N=20, P=0.033; at 60 m: T^2=7.51, N=20, P=0.05; at 90 m: T^2=49.78, N=20, P<0.001).

Releases at the secondary site suggest a twilight-informed perceptual range under 120 m, but the results are somewhat unclear (Fig. 4). As before, the mice released at 60 m were initially orientated towards the woods (*V* test: U=2.96, N=20, P=0.002), and after 10 m of movement their average location was significantly displaced away from the point of release (Hotelling's one-way test: T^2=21.06, N=20, P=0.002). Mice released at 120 m were not initially significantly orientated towards the woods (*V* test: U=1.09, N=20, NS), but they were significantly orientated parallel to the woods (*V* test: U=3.29, N=20, P=0.001). This parallel orientation was maintained during the first 10 m of movement, after

which their average location was significantly displaced away from the point of release (Hotelling's one-way test: T^2=10.18, N=20, P=0.022). However, the mice released at 120 m demonstrated no directional bias in net displacement after 60 m of travel (Hotelling's one-way test: T^2=4.88, N=20, NS). In contrast, after 60 m of travel, the average location of mice released at 60 m from the woods was highly displaced away from the point of release (Fig. 4; Hotelling's one-way test: T^2=12.69, N=20, P=0.001). Whatever the reason for the initial parallel orientation in mice released at 120 m (see below), they appeared largely to abandon this direction after their initial movements. We thus conclude that these mice did not perceive the woods as forested habitat. As before, mice not orientated towards the woods were also not significantly orientated towards home (V test: at 120 m: U= − 3.04, N=20, NS).

Once again, the data in Fig. 3 suggest that mice were initially moving in a direction intermediate between home and the woods. However, with the opaque side of the release mechanism facing away from home (Fig. 4), this tendency to 'veer homeward' disappeared. This strongly suggests that mice were initially orienting away from the opaque side of the release mechanism (Fig. 4). Interestingly, the tendency to orient away from the opaque cover declined as trails lengthened, but any bias associated with it remained neutral with respect to movements either towards or away from the woods. Orientation away from the opaque covering makes sense because mice should be more likely to move towards the portion of the field that they viewed throughout the prerelease holding period. Nevertheless, the influence of the woods on orientation was clearly evident in all but the 120-m releases.

Our results suggest that white-footed mice have the ability to assess the location of forest fragments during twilight hours and use that information during nocturnal navigation. We do not know whether wild mice use this strategy, because there is no information on the diel timing of dispersal events. However, such a 'look now and move later' strategy presumably would avoid the higher risks of predation during dispersal at twilight or under bright moonlight. Nevertheless, this strategy would work best for habitat patches in the immediate vicinity of the starting patch. Once a mouse moved beyond the area within view of its original position, it would experience the limited perceptual abilities typical of dark conditions.

GENERAL DISCUSSION

Behaviour plays an important role in animal ecology at the scale of ecological landscapes (Wennergren et al. 1995; Bowers et al. 1996; Lidicker & Koenig 1996; Lima & Zollner 1996; Wiens 1996). In fact, many landscape-level studies of animal ecology, particularly individual-based spatially explicit population models (Dunning et al. 1995), are essentially about the population-level consequences of behaviour. However, we know little about the behavioural phenomena upon which these models are constructed (Wennergren et al. 1995; Lima & Zollner 1996; Ruckelshaus et al. 1997). Perceptual range is one such behavioural phenomenon (Lima & Zollner 1996). For virtually all species, the extent of their 'landscape-level' perceptual abilities remains unknown, despite the likely influence of such abilities on the probability of successful dispersal.

Our study is not only one of the first to provide quantitative information on perceptual range, but it also demonstrates that perceptual range is not likely to be a fixed entity as assumed in population models. For many animals, perceptual range will likely vary with ecological conditions (see also Yeomans 1995). The level of ambient light is clearly one such condition influencing perceptual range in white-footed mice. Furthermore, such condition-dependent perceptual ranges set up the possibility for significant conflicts between increasing perceptual abilities and increasing predation risk during dispersal. When and how dispersal should proceed in animals facing such a conflict is unclear, although preliminary investigations of this trade-off using computer simulations indicate that optimal solutions are sensitive to both the density of habitat and the relationship between mortality and perceptual range (unpublished data).

Our observation that the perceptual abilities of white-footed mice increase with increasing ambient illumination may not directly translate into greater dispersal success under natural conditions. These mice are thought to disperse primarily during times of the year when crops are present in fields (Krohne et al. 1984; Cummings & Vessey 1994), and we have shown elsewhere that such visually obstructive environments decrease perceptual abilities substantially (Zollner & Lima 1997). Furthermore, mice dispersing across fields filled with crops might gradually familiarize themselves with a larger landscape through a series of smaller exploratory sallies rather than move in a single dispersal episode. None the less, any dispersal movements by white-footed mice will probably be constrained by perceptual abilities within the range of values described here.

As mentioned earlier, a critical assumption in our study is that the perception of forested habitat is equivalent to orientation towards it. If this assumption were not valid then our results might be interpreted as measuring the motivation of mice to move towards the woods rather than their ability to perceive the woods. However, trapping surveys and habitat choice experiments show clearly that white-footed mice perceive bare fields as unsuitable (Zollner & Lima 1997), hence they should orient towards any preferred habitat that they perceive. Data presented in this paper also support the above critical assumption. Consider the fact that mice released at 30 m on dark nights failed to move towards the woods (Fig. 1). One might argue that, under maximal darkness, these mice felt no particular urgency to move towards the woods (putting aside the fact that mice released at 10 m were apparently motivated to do so). However, mice provided with a twilight view and released under maximal darkness oriented towards the woods from as far away as 90 m (Fig. 3). Despite being released under maximal darkness, these twilight-informed mice did not linger in the field, but instead headed for the woods. This suggests that mice released at 30 m under maximal darkness without any

prior information simply failed to perceive the forest for what it was.

Our experiments were designed to control for the effects of factors other than the presence of the woods on the orientation of mice. As discussed above, one such factor was the orientation of the opaque covering on the release mechanism. Similarly, the experimental design controlled for the effects of other potentially influential factors such as the position of the moon, topography and wind direction. While the position of the moon varied during the moonlight experiments (depending on moon phase and time of night) any effects of moon position were equivalent for mice released at each distance. All release sites were also in flat fields far away from structures to ensure a distinctly greater horizon in the direction of the woods. Wind was not a factor in these experiments either as releases were conducted on calm nights. Finally, white-footed mice might possess some innate tendency for homing (Teferi & Millar 1993) but we detected no significant homeward orientation in mice released either within or beyond their ability to perceive the woods.

In conclusion, we clearly need a better understanding of the basic behavioural mechanisms that affect landscape-level ecological processes. However, it is not realistic to expect that a full understanding of such mechanisms can be developed for more than just a few species. We may nevertheless gain a better understanding of the interaction between behaviour and landscape-level ecological processes by studying species such as white-footed mice, which have received considerable attention in landscape ecology (Fahrig & Merriam 1985; Morris 1987; Merriam & Lanoue 1990; Bowers & Doley 1991, 1993; Heinen et al. 1998). Learning how animals acquire information and make decisions at the level of ecological landscapes is a crucial step towards the development of realistic, individually based models for population dynamics.

Acknowledgments

J. Deloughry, M. Evrard, J. Irwin, R. McClain, D. Morgan, R. Welsch and the Indiana State University kindly provided permission to use their properties in our experiments. E. Sprague, T. Hickox and C. Mathews provided assistance with the field work. P. Bednekoff, A. Brunet, N. Haddad, K. Krammer, V. Quinn and K. Zollner commented on the manuscript. The research presented here was described in Animal Research Protocol No. PZSL94, approved on 19 October 1994 by the Institutional Animal Care and Use Committee of Indiana State University. Funding for this work was provided by the Theodore Roosevelt Fund of the American Museum of Natural History, Indiana State University, and NSF grant IBN-9221925.

References

Batschelet, E. 1981. *Circular Statistics in Biology*. New York: Academic Press.

Barry, R. E. 1984. Effects of early experience on cue preferences of *Peromyscus leucopus*. *American Midland Naturalist*, **111**, 234–241.

Barry, R. E., Jr & Francq, E. N. 1980. Orientation to landmarks within the preferred habitat by *Peromyscus leucopus*. *Journal of Mammalogy*, **61**, 292–303.

Barry, R. E., Jr & Francq, E. N. 1982. Illumination preference and visual orientation of wild-reared mice, *Peromyscus leucopus*. *Animal Behaviour*, **30**, 339–344.

Bowers, M. A. 1990. Exploitation of seed aggregates by Merriams' kangaroo rat: harvesting rates and predatory risk. *Ecology*, **71**, 2334–2344.

Bowers, M. A. & Dooley, J. L., Jr. 1991. Landscape composition and the intensity of and outcome of two-species competition. *Oikos*, **60**, 180–186.

Bowers, M. A. & Dooley, J. L., Jr. 1993. Predation hazard and seed removal by small mammals: microhabitat versus patch scale effects. *Oecologia*, **94**, 247–254.

Bowers, M. A., Gregario, K., Brame, C. J., Matter, S. F. & Dooley, J. L., Jr. 1996. Use of space and habitats by meadow voles at the home range, patch and landscape scales. *Oecologia*, **105**, 107–115.

Brillhart, D. B. & Kaufman, D. W. 1991. Influence of illumination and surface structure on space use by prairie deer mice (*Peromyscus maniculatus bairdii*). *Journal of Mammalogy*, **72**, 764–768.

Brown, J. S., Kotler, B. P., Smith, R. J. & Wirtz, W. O. 1988. The effect of owl predation on the foraging behaviour of heteromyid rodents. *Oecologia*, **76**, 408–415.

Burt, W. H. 1940. Territorial behaviour and populations of some small mammals in southern Michigan. *Miscellaneous Publications of the Museum of Zoology, University of Michigan*, **45**, 1–58.

Clark, B. K. & Kaufman, D. W. 1991. Effects of plant litter on foraging and nesting behaviour of prairie rodents. *Journal of Mammalogy*, **72**, 502–512.

Clarke, J. A. 1983. Moonlight's influence on predator/prey interactions between short-eared owls (*Asio flammeus*) and deer mice (*Peromyscus maniculatus*). *Behavioral Ecology and Sociobiology*, **13**, 205–209.

Cooke, J. A. & Terman, C. R. 1977. Influence of displacement distance and vision on homing behaviour of the white-footed mouse *Peromyscus leucopus noveborcensis*. *Journal of Mammalogy*, **58**, 58–67.

Cummings, J. R. & Vessey, S. H. 1994. Agricultural influences on movement patterns of white-footed mice (*Peromyscus leucopus*). *American Midland Naturalist*, **132**, 209–218.

Drickamer, L. C. & Stuart, J. 1984. *Peromyscus*: snow tracking and possible cues used for navigation. *American Midland Naturalist*, **111**, 202–204.

Dunning, J. B., Stewart, D. J., Danielson, B. J., Noon, B. R., Root, T. L., Lamberson, R. H. & Stevens, E. E. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications*, **5**, 3–11.

Fahrig, L. 1988. A general model of populations in patchy habitats. *Applied Mathematics C.*, **27**, 53–66.

Fahrig, L. & Merriam, G. 1985. Habitat patch connectivity and population survival. *Ecology*, **66**, 1762–1768.

Gillis, E. A. & Nams, V. O. 1998. How red-backed voles find habitat patches. *Canadian Journal of Zoology*, **76**, 791–794.

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

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

Jekanoski, R. D. & Kaufman, D. W. 1995. Use of simulated herbaceous canopy by foraging rodents. *American Midland Naturalist*, **133**, 304–311.

Joslin, J. K. 1977. Visual cues used in orientation by white-footed mice, *Peromyscus leucopus*: a laboratory study. *American Midland Naturalist*, **98,** 308–318.

Kareiva, P. & Wennergren, U. 1995. Connecting landscape patterns to ecosystem and population processes. *Nature*, **373,** 299–302.

Kavaliers, M. & Galea, L. A. M. 1994. Spatial water maze learning using celestial cues by the meadow vole, *Mirotus pennsylvanicus*. *Behavioral Brain Research*, **61,** 97–100.

Kavaliers, M., Ossenkopp, K.-P., Prato, F. S., Innes, D. G. L., Galea, L. A. M., Kinsella, D. M. & Perrot-Sinal, T. S. 1996. Spatial learning in deer mice: sex difference and the effects of endogenous opioids and 60 Hz magnetic fields. *Journal of Comparative Physiology A,* **179,** 715–724.

Kavanau, J. L. 1967. Behaviour of captive white-footed mice. *Science*, **155,** 1623–1639.

Kavanau, J. L. 1968. Activity and orientational responses of white-footed mice. *Nature*, **218,** 245–253.

Kavanau, J. L. 1969. Influences of light on activity of small mammals. *Ecology*, **50,** 548–557.

Kavanau, J. L. & Havenhill, R. M. 1975. Compulsory regime and control of environment in animal behaviour III. Light level preferences of small nocturnal mammals. *Behaviour*, **59,** 203–224.

King, J. A. 1968. Psychology. In: *Biology of Peromyscus (Rodentia)* (Ed. by J. A. King), pp. 496–523. Stillwater, Oklahoma: American Society of Mammalogists.

King, J. A. 1975. Stimulus selection (light) in four subspecies of deer mice (*Peromyscus maniculatus*). *Journal of Interdisciplinary Cycle Research*, **6,** 267–278.

King, J. A. & Vestal, B. M. 1974. Visual acuity of *Peromyscus*. *Journal of Mammalogy*, **55,** 238–243.

Kotler, B. P. 1984. Risk of predation and the structure of desert rodent communities. *Ecology*, **65,** 689–701.

Kotler, B. P., Brown, J. S. & Hasson, O. 1991. Factors affecting gerbil foraging behaviour and rates of owl predation. *Ecology*, **72,** 2249–2260.

Kotler, B. P., Blaustein, L. & Brown, J. S. 1992. Predator facilitation: the combined effect of snakes and owls on the foraging behaviour of gerbils. *Annales Zoologici Fennici*, **29,** 199–206.

Krohne, D. T., Dubbs, B. A. & Baccus, R. 1984. An analysis of dispersal in an unmanipulated population of *Peromyscus leucopus*. *American Midland Naturalist*, **112,** 146–156.

Lemen, C. A. & Freeman, P. W. 1985. Tracking mammals with fluorescent pigments: a new technique. *Journal of Mammalogy*, **66,** 134–136.

Lidicker, W. Z., Jr & Koenig, W. D. 1996. Responses of terrestrial vertebrates to habitat edges and corridors. In: *Metapopulations and Wildlife Conservation* (Ed. by D. R. McCullough), pp. 85–111. Washington, D.C.: Island Press.

Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioural, reproductive, and ecological perspectives. *Advances in the Study of Behavior*, **27,** 215–290.

Lima, S. L. & Zollner, P. A. 1996. Towards a behavioural ecology of ecological landscapes. *Trends in Ecology and Evolution*, **11,** 131–135.

Liu, J., Dunning, J. B., Jr & Pulliam, H. R. 1995. Potential effects of a forest management plan on Bachmans sparrows (*Aimophila aestivalis*): linking a spatially explicit model with GIS. *Conservation Biology*, **9,** 62–75.

Longland, W. S. & Price, M. V. 1991. Direct observations of owls and heteromid rodents: can predation risk explain microhabitat use? *Ecology*, **72,** 2261–2273.

McMillan, B. R. & Kaufman, D. W. 1994. Travel path characteristics for free-living white-footed mice (*Peromyscus leucopus*). *Canadian Journal of Zoology*, **73,** 1474–1478.

Merriam, G. & Lanoue, A. 1990. Corridor use by small mammals: field measurements for three experimental types of *Peromyscus leucopus*. *Landscape Ecology*, **4,** 123–131.

Mitton, J. 1991. *A Concise Dictionary of Astronomy*. New York: Oxford University Press.

Morris, D. W. 1987. Ecological scale and habitat use. *Ecology*, **68,** 227–234.

Pulliam, H. R., Dunning, J. B., Jr & Liu, J. 1992. Population dynamics in complex landscapes: a case study. *Ecological Applications*, **2,** 165–177.

Reed, J. M. & Dobson, A. P. 1993. Behavioural constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution*, **8,** 253–256.

Ruckelshaus, M., Hartway, C. & Kareiva, P. 1997. Assessing the data requirements of spatially explicit dispersal models. *Conservation Biology*, **11,** 1298–1306.

Schippers, P., Verboom, J., Knappen, J. P. & van Apeldoorn, R. C. 1996. Dispersal and habitat connectivity in complex heterogeneous landscapes: an analysis with a GIS-based random walk model. *Ecography*, **19,** 97–106.

Smith, A. T. & Peacock, M. M. 1990. Conspecific attraction and the determination of metapopulation colonization rates. *Conservation Biology*, **4,** 320–323.

Sheppe, W. 1965. Dispersal by swimming in *Peromyscus leucopus*. *Journal of Mammalogy*, **46,** 336–337.

Stamps, J. A. 1991. The effects of conspecifics on habitat selection in territorial species. *Behavioral Ecology and Sociobiology*, **28,** 29–36.

Stamps, J. A., Buechner, M. & Krishnan, V. V. 1987. The effects of edge permeability and habitat geometry on emigration from patches of habitat. *American Naturalist*, **129,** 533–552.

Svihla, A. 1932. A comparative life-history study of the mice of the genus *Peromyscus*. *Miscellaneous Publication of the Museum of Zoology, University of Michigan*, **24,** 1–39.

Teferi, T. & Millar, J. S. 1993. Long distance homing by the deer mouse, *Peromyscus maniculatus*. *Canadian Field Naturalist*, **107,** 109–111.

Travers, S. E., Kaufman, D. W. & Kaufman, G. A. 1988. Differential use of experimental habitat patches by foraging *Peromyscus maniculatus* on dark and bright nights. *Journal of Mammalogy*, **69,** 869–872.

Turner, M. G., Wu, Y., Romme, W. H. & Wallace, L. L. 1993. A landscape simulation of winter foraging by large ungulates. *Ecological Modelling*, **69,** 163–184.

Turner, M. G., Wu, Y., Wallace, L. L., Romme, W. H. & Benkert, A. 1994. Simulating winter interactions among ungulates, vegetation, and fire in northern Yellowstone Park. *Ecological Applications*, **4,** 472–496.

Vásquez, R. A. 1994. Assessment of predation risk via illumination level: facultative central place foraging in the cricetid rodent *Phyllotis darwini*. *Behavioral Ecology and Sociobiology*, **34,** 375–381.

Vásquez, R. A. 1996. Patch utilization by three species of chilean rodents differing in body size and mode of locomotion. *Ecology*, **77,** 2343–2351.

Wennergren, W., Ruckelshaus, M. & Kareiva, P. 1995. The promise and limitations of spatial models in conservation biology. *Oikos*, **74,** 349–356.

Whitaker, J. O., Jr. 1982. *Key to the Vertebrates of the Eastern United States*. 2nd edn. Minneapolis, Minnesota: Burgess.

Wiens, J. A. 1996. Wildlife in patchy environments: metapopulations, mosaics, and management. In: *Metapopulations and Wildlife Conservation* (Ed. by D. R. McCullough), pp. 85–111. Washington, D.C.: Island Press.

Wiens, J. A., Stenseth, N. C., Van Horne, B. & Ims, R. A. 1993. Ecological mechanisms and landscape ecology. *Oikos*, **66,** 369–380.

Wolfe, J. L. & Summerlin, C. T. 1989. The influence of lunar light on nocturnal activity of the old-field mouse. *Animal Behaviour*, **37,** 410–414.

Yeomans, S. R. 1995. Water-finding in adult turtles: random search or oriented behaviour? *Animal Behaviour*, **49,** 977–987.

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