How does habitat structure affect activity and use of space among house mice?

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For small mammals that are vulnerable to predation, the protection provided by physical structuring within the habitat is important in determining suitable nest or resting sites but little is known about how different aspects of structure affect use of the habitat more generally. We examined the effects of ground-level structure (open/complex), overhead cover (present/absent) and the distribution of protected nest sites and food (clumped together/scattered) on activity and use of space among house mice, Mus domesticus, in enclosures. Adult pairs were housed in eight habitat types differing in arrangement of nestboxes, bricks and cover sheets, and their location was monitored under infrared light every 0.5 s over 4 h during the dark period. The mice spent much more time within protected nest sites and were more restricted in use of different sites within habitats that had little ground-level structure and no overhead cover. Much wider use was made of structurally complex habitats. Complex ground-level structure had the greatest impact on emergence from protected nest sites and use of space, since mice preferred to stay close to, or on top of, walls and other objects when undisturbed. The influence of overhead cover on normal activity depended on the extent of ground-level structure and origin of the mice, but, when disturbed by an experimenter, mice sheltered under overhead cover or in enclosed nest sites. Preference between nest sites depended on accessibility from under overhead cover and proximity to enclosure walls. We found almost no sex differences in activity or use of space.

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Risk of predation is an important factor determining habitat choice, activity and movement patterns of small mammals such as rodents (e.g. Kotler 1984; Brown et al. 1988) and many small mammals avoid open habitats under increased risk of predation (Brown & Alkon 1990; Dickman 1992; Bowers & Dooley 1993; Bowers et al. 1993; Hughes et al. 1994). Small mammals are usually highly dependent on safe nesting sites that provide physical protection, such as holes in trees, in the ground or in crevices between rocks (Barry & Francq 1980; Hansson 1982; Pennycuik et al. 1987), and since they must always return to a safe site when resting, the distribution of safe sites within habitats is likely to have a strong impact on the pattern of use of the home area.

When away from the physical protection offered by nest sites, rodents foraging and moving about usually prefer areas with overhead cover provided by vegetation just above the ground, or more solid structures such as logs, large stones or overhanging banks of earth. While all types of overhead cover make them much less visible to predators, solid overhead cover also limits access for larger mammalian and avian predators, thus providing direct protection (e.g. Rosenzweig 1973; Gray et al. 1998; Manson & Stiles 1998). The amount and distribution of overhead cover may therefore affect not only predation risk (and thus mortality rates) but also the ‘usable’ area within a habitat, allowing animals access to food resources that would otherwise be much more difficult or too dangerous to exploit (Gray & Hurst 1998).

Other studies have indicated that ground-level structuring also provides a form of protection from predators and allows animals to make more extensive use of the habitat (e.g. Barry & Francq 1980; Kotler 1984). Thus, rodents are often reluctant to venture out into open spaces and instead prefer to remain close to walls or objects, which provide vertical cover. In laboratory experiments, house mice, Mus domesticus, prefer areas with even a small amount of ground-level complexity to open areas (Gray et al. 2000). Mice follow predictable runways along edges where physical structuring is aligned but follow more complex and variable pathways around scattered objects.
This does not appear to be a thigmotaxis, in which rodents attempt to maintain contact with vertical surfaces, since rodents readily follow pathways along the top of walls, branches or other objects. Staying close to vertical surfaces may reduce predation risk in a number of ways, for example, by minimizing the shadows cast when moving about, by reducing the number of directions from which a predator can approach and by increasing the likelihood that a crevice in which to hide will be close by. Moving along the tops of objects may also allow mice to drop quickly over the edge to take evasive action in three dimensions rather than two.

A number of studies have addressed the effects of habitat structure and predation risk on movement patterns and feeding activity indirectly, for example by trapping (Dickman 1992; Jorgensen & Demarais 1999; Torre & Bosch 1999; Jonsson et al. 2000), recording the presence of rodent tracks on sand or smoked tiles under and away from shrubs (Lagos et al. 1995; Falkenberg & Clarke 1998), following trails left by rodents marked with coloured fluorescent pigment (Lagos et al. 1995), comparing the number and length of runways made by small mammals in different types of vegetation (Lagos et al. 1995) or by comparing bait taken under vegetation cover and in the open (Crowcroft 1959; Bowers & Dooley 1993). However, there have been few attempts to measure directly how different aspects of habitat structure affect activity and use of space, despite the potential importance of this for understanding differences in access to resources and ease of resource defence in different habitat types, and thus the density and distribution of animals that different habitats will support.

We examined the relative importance of the distribution of protected nest sites, presence of overhead cover and complexity of ground-level structure in determining activity and use of the habitat by house mice, and how these interact, by manipulating each of these three habitat factors independently in laboratory enclosures. House mice prefer to live commensally with humans in buildings where they can gain access to animal feed or stored foods and are protected from harsh weather conditions (Berry 1981). In addition to dogs and cats, humans are the main ‘predators’ under these conditions, maintaining a strong pressure on mice to remain hidden from view and to have ready access to safe nest sites that provide a high degree of physical protection (e.g. Southern 1954). Since stored foods or animal feed are generally abundant, individual territories are often only a few square metres (Anderson 1961; Mackintosh 1981; Hurst 1986, 1987). Such human-built environments are readily modelled and manipulated in the laboratory.

We predicted that mice would be much more restricted in their use of open habitats, particularly when there was no overhead cover and little ground-level complexity and protected nest sites were located in only some areas of the habitat. Under these conditions, we expected mice of both sexes to spend much time within or close to their nest sites, or close to the enclosure walls. In contrast, we expected mice to make much wider use of physically complex habitats containing overhead cover, extensive ground-level structure and widely scattered nest sites, and to spend less time within the shelter of protected nest sites. However, we could not predict which of the three factors was likely to be most important in determining activity and use of space, how they might interact, or how strong the effects on mouse behaviour would be. Not only does this have important applications for understanding detailed use of the microhabitat of a serious and world-wide pest species, it is also important for understanding the extent to which physical structure can influence activity and use of the habitat by animals that are highly vulnerable to predation.

METHODS

Habitat Types

We created eight habitat types within separate enclosures by manipulating the complexity of ground-level structure (‘open’ or ‘complex’), overhead cover (‘cover’ or ‘no cover’) and distribution of nest site and food resources (‘clumped’ or ‘scattered’). Enclosures (1.2 × 2.4 m and 0.8 m high) constructed from melamine-covered chipboard were each divided in two by a central opaque Perspex partition to give pairs of test enclosures, each measuring 1.2 × 1.2 m. Each test enclosure contained six nestboxes (12 cm diameter and 8 cm high, filled with shredded paper nest material), a bowl of water, a water bottle (removed during filming) and 40 concrete bricks (20 × 3 × 3 cm). The arrangement of these bricks differed according to the habitat type. In habitats with complex ground-level structure the bricks were distributed across the enclosure floor at different angles to produce a complex spatial arrangement; in open habitats all of the bricks were lined up along the enclosure walls (Fig. 1). To create a ‘clumped’ resource distribution, the nestboxes were placed at one end of each enclosure (away from the partition between neighbours) in two rows of three with entrance holes aligned and with a food dish containing wheat placed near each row. For a ‘scattered’ resource distribution, the nestboxes in each row were spaced out maximally between the partition and back wall of the enclosure with the entrance holes facing towards the centre for the middle two nestboxes and towards the side walls for the outer two pairs of nestboxes, and wheat grains were scattered evenly across the floor. Half of the enclosures also contained two clear horizontal Perspex sheets (30 × 118 cm and 3 mm thick) as low overhead cover under which the mice could shelter. These were placed 3 cm above the enclosure floor supported by the bricks, one against the right side wall and the other in the central area of the enclosure such that they abutted a row of nestboxes (Fig. 1b). In habitats with open ground-level structure, two of the bricks were replaced by eight quarter bricks to hold up the edges of the two cover sheets.

To ensure maximum contrast between the animals and the background for image analysis, the enclosures were white and all objects within the enclosures were either in clear Perspex (overhead cover sheets, food dishes, water dish) or sprayed with white car paint (nestboxes, bricks). This light background is unlikely to have influenced...
behaviour as mice were recorded during the dark period under infrared lights.

Subjects

Six replicate male–female pairs of mice were housed in each of the eight habitat types, which represented all combinations of ground-level structuring, overhead cover and resource distribution. Two additional replicate pairs were housed in open habitats with scattered resources and no cover by mistake, so we gained data for 50 pairs of mice in total. We used 50 male and 50 female first- or second-generation captive-born house mice. Of these, 30 males and 30 females descended from mice captured from several arable and livestock farms in Nottinghamshire, U.K., while the rest originated from sites in Cheshire (an agricultural college, a field station, a zoo and a farm). This corresponded to a move of our laboratory from Nottingham to Liverpool after approximately two-thirds of the replicates for each habitat type had been recorded. All enclosures and equipment were moved and reconstructed in a room purpose built to be as similar as possible to the original set-up. Of the mice originating from Cheshire, 11 males and 14 females were conceived in the wild and born in captivity from dams captured while pregnant. All other mice were bred in captivity from pairs or trios. Before and after the trials the mice were housed in polypropylene cages (42 × 25 cm and 12 cm high) with wire-mesh tops, on peat substrate with shredded paper nest material and maintained on ad libitum food (Harland Teklad Rodent Breeder 9607) and water. Captive-bred Nottinghamshire mice were reared with both parents. Since most of the Cheshire mice were conceived in the wild, any Cheshire sires were removed from the breeding cage as soon as the mother was visibly pregnant. All mice were weaned into single-sex groups of siblings (females stayed with their mother) at 4 weeks of age and were 20–24 weeks old at the beginning of trials. During the week before trials, we individually marked the mice with a PIT tag (12 mm, Francis Scientific Instruments, Cambridge, U.K., injected subcutaneously in the loose skin over the shoulders) and bleached the dorsal fur with commercial hair dye (Nottinghamshire mice with Bblonde, JeromeRussell Plc, London, U.K.; Cheshire mice with Nordic Colors Lightening Cream, Schwarzkopf & Henkel Cosmetics, Düsseldorf, Germany) to allow individuals to be recognized from videotapes. Mice within each pair originated from either Nottinghamshire or Cheshire stock but were not closely related. Males of Nottinghamshire stock were each paired up with an unfamiliar female in a breeding cage for 4 days before both were introduced into their experimental enclosure. Aggression levels were higher among mice of Cheshire mice stock, so each pair was introduced in the enclosure rather than within cages as this reduced or eliminated initial aggression towards the female. Throughout the experiment, mice were maintained on a reversed-phase light:dark cycle of 12:12 h with white lights coming on at 14:00 hours. During the dark phase all lights were off except during maintenance and handling, which were always carried out during the dark phase under red lights. At the end of the experiment, mice were kept in their enclosures for further behavioural research.

Assessment of Activity and Spatial Location

Pairs of mice were introduced into separate enclosures and left for 5–6 days to become familiar with the habitat. During this time we subjected the mice to a number of scent-marking and odour preference tests which involved capturing them in Perspex handling tubes at least seven times each (mice were exposed briefly to the scents of an unfamiliar male and female, data not presented here). They thus had the opportunity to become familiar with the protection offered by the nestboxes and the Perspex sheets during capture. Each pair of mice was then videoed for the last 4 h of the dark phase under infrared lighting. One hour into the recording an experimenter entered the room and clicked her fingers over the enclosures to simulate a predation threat.

We sampled the location of each mouse every 0.5 s using the Ethovision motion analysis system (version 1.90, Noldus, Wageningen, The Netherlands) to extract accurate X and Y coordinates from videotapes. The mice
were distinguished by Ethovision on the basis of the size of the mouse's dark image against a light background when not within a nestbox. Initially, we attempted to ensure that the female always appeared smaller than the male by bleaching the fur on her back, shoulders and rump, so that each animal within a pair could be discriminated automatically. However, Ethovision often failed to identify the male and female correctly since mice changed shape when rearing up or when they entered or left a nestbox. Occasionally, the Ethovision system also incorrectly recorded a location when no mouse was there, apparently because of interference in the recorded video signal. To ensure the accuracy of our data, we thus transcribed manually the exact time that each animal entered or left a nestbox. This allowed us to identify when each individual was active and being tracked. The raw coordinate data collected by Ethovision were then matched with these activity data and we used this to identify records when either the male or the female was active separately (i.e. the other member of a pair was within a nestbox). We used this subset of data to analyse individual use of space when mice were active in the absence of interference from their mate. We also examined behaviour when both mice were active simultaneously, but in these records we could not distinguish reliably between the coordinates of the male and female so we combined data for both animals. The number of coordinates collected per pair or individual thus varied according to how long animals were active together or separately within the 4-h recording period (Table 1). The number of coordinates available when each mouse was active alone was similar across habitats, between the sexes and the two origins of mice. More data were generally available when both mice were active simultaneously, particularly in complex habitats. In enclosures with overhead cover, we also distinguished whether mice were above or below the cover by recording manually from video records the time spent by each animal above and below the clear Perspex sheets. In all enclosures, we also recorded any bouts when mice slept outside the nestboxes.

### Data Analysis

Three male and two female mice showed abnormal stereotypical behaviour when active, often running in fixed circles around the enclosures (all except one female were from Nottinghamshire stock). Since only two of these five mice were found in the same habitat type, it is unlikely that habitat type had any effect on this behaviour, which presumably developed during cage rearing before the experiment (e.g. Jerussi & Hyde 1985). Data for these mice were thus excluded from analyses of use of space.

We calculated the total proportion of the recording period that each individual spent outside nestboxes as an index of total activity. To assess differences in the relative use of different areas when mice were active, we calculated the time spent in specific locations as a proportion of the total time spent outside nestboxes, both for each individual active alone and when both mice were active simultaneously. This relative use of different areas when active was thus independent of the total time that animals were active. We then calculated the total proportion of each recording period spent in specific locations per mouse, using data on individual activity (time outside nestboxes) and the proportion of coordinates in specific locations when individual mice were active alone. This analysis examined the combined effects of habitat type on both time spent active and the relative use of different areas when active. The specific sites compared between enclosures were: near to side walls (within 12 cm of each of the two side walls); the central area of the enclosure (a 24-cm strip running down the centre of the enclosure

### Table 1. Number of coordinates available per pair within different habitat types (median with minimum and maximum number of coordinates in parentheses)

<table>
<thead>
<tr>
<th>Habitat type*</th>
<th>No. of pairs</th>
<th>Male only active (male coordinates)</th>
<th>Female only active (female coordinates)</th>
<th>Both mice active</th>
<th>Total per pair active or inactive</th>
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<tbody>
<tr>
<td>Open, clumped, no cover</td>
<td>6</td>
<td>1586</td>
<td>1345</td>
<td>1940</td>
<td>53762</td>
</tr>
<tr>
<td></td>
<td></td>
<td>(123–2727)</td>
<td>(359–5376)</td>
<td>(116–24 638)</td>
<td>(31 074–57 334)</td>
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<tr>
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<td>5008</td>
<td>4808</td>
<td>7398</td>
<td>54 767</td>
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<tr>
<td>Open, scattered, no cover</td>
<td>8</td>
<td>3197</td>
<td>6441</td>
<td>2688</td>
<td>54 386</td>
</tr>
<tr>
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<td>6</td>
<td>2403</td>
<td>1820</td>
<td>3640</td>
<td>55 426</td>
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<td></td>
<td>(112–11 170)</td>
<td>(1291–16 794)</td>
<td>(0–46 812)</td>
<td>(42 526–56 640)</td>
</tr>
<tr>
<td>Complex, clumped, no cover</td>
<td>6</td>
<td>2865</td>
<td>1820</td>
<td>3928</td>
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<td></td>
<td></td>
<td>(265–13 299)</td>
<td>(1291–16 794)</td>
<td>(0–46 812)</td>
<td>(42 526–56 640)</td>
</tr>
<tr>
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<td>3114</td>
<td>16 537</td>
<td>50 781</td>
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<td></td>
<td></td>
<td>(307–10 104)</td>
<td>(1195–12 536)</td>
<td>(28–45 084)</td>
<td>(40 642–54 598)</td>
</tr>
<tr>
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<td>4652</td>
<td>6843</td>
<td>50 907</td>
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<tr>
<td></td>
<td></td>
<td>(1823–10 236)</td>
<td>(315–10 427)</td>
<td>(1916–39 032)</td>
<td>(41 998–56 104)</td>
</tr>
<tr>
<td>Complex, scattered, cover</td>
<td>6</td>
<td>5531</td>
<td>4040</td>
<td>11 614</td>
<td>54 140</td>
</tr>
</tbody>
</table>

*Ground-level structure, resource distribution, overhead cover.
between the nestboxes, excluding edges within 12 cm of the front and back walls; the edge and middle cover areas corresponding to the location of the two Perspex cover sheets in enclosures where overhead cover was present (two 30-cm-wide strips running between a side wall and one row of nestboxes or between the mid-line and the other row of nestboxes; Fig. 1b); nestbox areas (an area of 15 × 15 cm centred over each nestbox); away from enclosure walls (anywhere not within 12 cm of the enclosure walls).

Data on the proportion of time active or spent in specific locations approximated normal distributions (Kolmogorov–Smirnov tests: NS), although some variables required logarithmic transformation as stated below. Repeated measures ANOVAs examined the between-subjects effects on time spent out of nestboxes and mean duration of bouts out of nestboxes of ground-level structure (open or complex), overhead cover (cover or no cover), resource distribution (clumped or scattered) and origin of the mice (Nottinghamshire or Cheshire), while also checking for any within-subjects effects of sex. Univariate ANOVAs examined the effects of ground-level structure, overhead cover, resource distribution, sex and origin of the mice on (1) the proportion of time spent in different locations when each mouse was active alone, (2) the proportion of the total recording period spent in different locations and (3) mean distance moved between successive coordinates. We also checked whether use of space was similar when both mice were active simultaneously. In this case, we could not assign coordinates accurately to the male or female and sex was not included in the analysis. A post hoc, univariate ANOVA compared the effects of structure (ground-level and overhead), resource distribution, sex and origin of the mice on the proportion of the total recording period spent in different locations in the most open (open ground-level structure with no overhead cover) and the most structured (complex ground-level structure with overhead cover) habitat types. In each analysis, we had only sufficient data to examine interactions between a maximum of three between-subject effects.

Time spent within each nestbox did not approximate normality and could not be transformed for parametric analysis. Total time spent in each of the six nestboxes was thus ranked 1–6 and averaged for each pair of mice. Using a Page test for ordered alternatives (Siegel & Castellan 1988) we tested whether the mice chose nestboxes according to two criteria: (1) accessibility from under overhead cover (where present), and (2) proximity to two enclosure walls (i.e. the sum of the direct distance to the nearest two walls), by ranking the nestboxes according to these criteria in each habitat type and comparing this ranking with the preference ranks shown by the mice. Unless stated, all data were analysed using SPSS versions 9 and 10 (SPSS Inc., Chicago, Illinois, U.S.A.). Means are given ± SE.

RESULTS

Use of Habitat while Active

Side walls

Ground-level complexity significantly reduced the proportion of time that mice outside nestboxes (i.e. active) spent close to the side walls of enclosures ($F_{1,67}=18.3, P<0.001$). Overhead cover also reduced such ‘wall-seeking’ behaviour ($F_{1,67}=5.54, P<0.025$), but this had much less effect than ground-level complexity, and overhead cover only tended to reduce the proportion of time near side walls in open habitats without much ground-level complexity (interaction between ground-level complexity and overhead cover: mice active alone: $F_{1,67}=3.65, P<0.06$; both mice active together: $F_{1,31}=4.19, P<0.05$; Fig. 2). The proportion of time spent near side walls was similar whether mice were active alone or together (Fig. 2) and there were no differences according to the origin of the mice.

Centre of enclosure

Mice of both sexes spent relatively little of their active time in the centre of the enclosure away from both the nestboxes and outer walls (on average, mice spent 7.2 ± 0.6% of their active time in the central area, representing 16% of total floor area), making similar use of the central area whether active alone or together. Use of the central area was increased by ground-level complexity (9.0 ± 1.1% versus 6.2 ± 0.7% of time active when individuals were out alone; effect of ground-level complexity: $F_{1,67}=11.44, P<0.001$, data log transformed for analysis), although it was still not proportional to the available area. By contrast, overhead cover had no significant effects on use of the central area. Resource distribution appeared to have a minor effect depending on the origin and sex of the mice (interaction between resource distribution, sex and origin: $F_{1,67}=4.10, P<0.05$), but post hoc analysis within mice of different origin revealed no

Figure 2. Percentage of active time spent within 12 cm of the side walls by males when out alone (●), females when out alone (●) and males and females when out together (●), according to ground-level complexity (open/complex) and the presence of overhead cover. Dashed line indicates that the area near the side walls represented 20% of the total area.
significant effects of resource distribution or interactions with other factors.

Covered areas

To examine whether mice used areas more when these were protected by overhead cover, we compared the proportion of time that active mice spent in the two areas that were covered by Perspex sheets with time spent in the equivalent areas of enclosures that had no overhead cover. Mice spent $14 \pm 1$% of their active time in the central cover area (25% of floor area) and this was not affected by the presence of overhead cover (effect of cover: $F_{1,67}=2.88$, NS, data log transformed for analysis). In contrast, use of the cover area that abutted a side wall depended on an interaction between the presence of overhead cover and ground-level complexity ($F_{1,67}=9.72$, $P<0.005$, data log transformed for analysis). In open habitats that had little ground-level structure, overhead cover increased the time that active mice spent in the 30-cm-wide strip running parallel to the side wall from $16 \pm 2$ to $40 \pm 8$%, indicating that activity was strongly focused in this covered edge area, which represented only 25% of the total enclosure floor area. Complex ground-level structure also increased activity in the area to $25 \pm 2$% but when there was ground-level complexity throughout the habitat, overhead cover did not increase the attractiveness of the covered area any further (even though cover increased the total area above and below the edge cover to 33% of the total surface area). Similar differences were apparent when both mice were active together. Overhead cover thus increased use of an open area with no ground-level structure that was otherwise avoided, but not if the cover was surrounded by open areas on both sides.

The presence of overhead cover sheets effectively doubled the surface area available to mice in the covered sites since they spent time on top of the cover as well as beneath it. There was an unexpected difference in the ratio of time spent above and below the cover sheets according to the origin of the mice ($F_{1,22}=12.78$, $P<0.0025$). All mice spent a similar time above the cover sheets, but while Nottinghamshire mice spent as much time below the cover as above, Cheshire mice spent much more time below the cover (Fig. 3). This difference in use of cover was evident regardless of ground-level structuring.

Resource areas

Overall, active mice spent $20 \pm 1$% of their time on or close to nestboxes (occupying 9.4% of enclosure floor area), but this depended on a significant interaction between the distribution of nestboxes and the presence or absence of overhead cover ($F_{1,67}=10.94$, $P<0.0025$). Mice spent least time on clumped nestboxes if there was no overhead cover but least time on scattered boxes when there was overhead cover (Fig. 4). When nestboxes were clumped, post hoc analysis showed that overhead cover slightly increased the proportion of time that active mice spent on the nestboxes ($F_{1,41}=5.1$, $P<0.05$). More importantly, though, clumped nestboxes were arranged in two groups (Fig. 1a) and mice spent twice as much time on the group of boxes that was slightly closer to the enclosure side wall (18 cm versus 36 cm from a side wall) regardless of whether overhead cover was present. When nestboxes were scattered, overhead cover had a highly significant effect but in the opposite direction ($F_{1,46}=10.58$, $P<0.0025$): active mice spent much more time on scattered nestboxes when there was no overhead cover. This was due to a considerable increase in time spent on the two nest sites that touched the front enclosure wall (the other four nest sites did not touch an outer wall). These two boxes were preferred sites even when overhead cover was present, presumably because these were the closest boxes to an outer wall. Ground-level
complexity had no significant effects on time spent on nestboxes.

Since active mice focused much of their activity around the nestboxes, resource distribution had a strong effect on their general location when active. When nest and food resources were clumped together near the back wall of each enclosure, mice spent significantly more of their active time in the back than in the front half of each enclosure (59 ± 2% time active: $t_{44}=4.53$, $P<0.001$). However, this bias was due entirely to time spent on or close to the nestboxes. When time on the nestboxes themselves was excluded, there was no difference in activity between the two halves of the enclosure even though food was present only in two dishes near to the back wall (40 ± 2% time active in back half, 41 ± 2% in front half: $F_{1,29}=0.06$, NS). Food thus appeared to have little effect on their overall distribution of activity and, although mice spent much time sitting on top of the nestboxes themselves, they did not stay in the vicinity when active around the enclosure.

When nest and food resources were scattered, there was a significant bias in the opposite direction: mice spent more of their active time in the front than in the back half of each enclosure (58 ± 2.5% time active: $t_{60}=3.35$, $P<0.005$), although there was also a significant difference in bias between males and females ($F_{1,38}=4.58$, $P<0.05$), since only males showed a significant preference for the front half of enclosures. Again, the bias was due entirely to time spent on or close to the nestboxes, four of which were sited in the front half of the enclosure, including the most preferred boxes sited against the front wall. Excluding time on the nestboxes, mice spent 36±2% of their time in the back half and 42±2% in the front half of enclosures ($F_{1,38}=2.18$, NS).

**Movement**

We calculated the mean distance moved between successive coordinates recorded every 0.5 s (data log transformed for analysis) as an indicator of how much mice moved about when active. The mean distance moved was much greater for Cheshire mice than for Nottinghamshire mice (effect of origin: $F_{1,67}=12.67$, $P<0.001$). There was also a significant interaction between ground-level complexity and resource distribution ($F_{1,67}=4.16$, $P<0.05$) because movement was lower in habitats where there was both complex ground-level structuring and scattered resources than in other types of habitat (Fig. 5). Movement was also reduced by the presence of overhead cover ($F_{1,67}=4.45$, $P<0.05$).

**Response to human disturbance**

In habitats that provided overhead cover, 33 mice were out of their nestboxes when an experimenter clicked her fingers over the enclosure 1 h into the recording. Of these, 25 (75.8%) fled and hid under the Perspex sheets (a response that was not affected by ground-level complexity). Of these, 11 hid under the central cover sheet and 14 under the edge cover. Six mice (18.2%) fled to a nestbox and another two (6%) hid behind nestboxes. Of the 32 animals that were out in enclosures that had no overhead cover other than nestboxes, 24 (75%) fled to nestboxes and eight (24%) hid behind nestboxes.

Responses were similar regardless of sex or origin. In habitats with overhead cover, mean time to re-emergence was $142.36 ± 62.50$ s from under the Perspex sheets ($N=25$). Re-emergence time from nestboxes was $54.50 ± 26.46$ s ($N=6$) in habitats with overhead cover and $201.50 ± 58.10$ s ($N=24$) in habitats without overhead cover, but this difference was not statistically significant (Mann–Whitney U-test: $U=43.50$, NS). Ground-level complexity and resource distribution did not appear to affect response to human disturbance.

**General Activity**

Mice almost invariably used the nestboxes when resting. Of the 100 experimental mice, only three were observed sleeping elsewhere when they rested under the overhead cover (four bouts in 200 h of video taken during the dark period). Thus, mice were almost always active when not within nestboxes. The distribution of nest sites did not affect the proportion of time that mice spent outside nestboxes ($F_{1,36}=1.54$, NS), and there was no difference in activity between males and females ($F_{1,36}=0.12$, NS). However, there was a significant interaction between the effects of ground-level complexity, overhead cover and the origin of the mice ($F_{1,36}=5.42$, $P<0.05$). Mice of different origin were thus analysed separately.

Cheshire mice spent significantly more time out of nestboxes in habitats with complex ground-level structure ($F_{1,13}=6.32$, $P<0.05$). Their activity was not influenced by overhead cover ($F_{1,13}=0.12$, NS; interaction between ground-level complexity and overhead cover: $F_{1,13}=0.29$, NS). Mice spent only 26 ± 4% of the dark
period away from protected resting sites in open habitats but this rose to 60 ± 8% with complex ground-level structuring (Fig. 6a). In contrast, Nottinghamshire mice spent a high proportion of time out of nestboxes (57 ± 7%) only when there was both ground-level complexity and overhead cover, spending only 35 ± 3% time out in other types of habitat (interaction between complexity and cover: $F_{1,23}=11.01, P<0.005$; Fig. 6b). Thus, all mice spent little time outside nestboxes in open habitats while physical structuring markedly increased activity. The difference between Cheshire and Nottinghamshire mice was in their willingness to spend time outside protected resting sites in habitats that had ground-level structure but not overhead cover. These differences were similar in males and females (Fig. 6).

The mean duration of each bout when mice emerged from nestboxes (log transformed for parametric analysis) was increased by both ground-level complexity ($F_{1,56}=15.41, P<0.001$) and overhead cover ($F_{1,56}=9.66, P<0.01$; Fig. 6c). In contrast to the total time spent out, overhead cover increased the length of individual bouts outside nestboxes in both open and complex habitats. There were no effects of sex or origin of the mice on bout duration.

### Preference between Nest Sites

Time spent within each nestbox was strongly non-normal, with mice often spending prolonged periods in one or two boxes and spending little if any time in others. Nestbox preferences were thus ranked 1–6 and averaged for each pair of mice. Figure 7 shows the position of the nestboxes with the highest ($\geq 4$) and the lowest ($\leq 2.5$) mean preference ranks for each habitat type. In habitats with no overhead cover, mice appeared to prefer nestboxes with the shortest distance to two enclosure walls and to avoid those furthest from the walls. However, mice in habitats with overhead cover primarily appeared to prefer nestboxes that could be entered from underneath the overhead cover, and of the three nestboxes that could be entered in this way, the ones closest to two side walls were preferred. We therefore checked whether preference matched those predicted by distance from the nearest enclosure walls or proximity of the entrance to overhead cover. Preferences in habitats without overhead cover matched those predicted when nestboxes were ranked according to their proximity to the nearest two walls (Page test: open enclosures: $L=1115, N=14, P<0.01$; complex enclosures: $L=951, N=12, P<0.01$). However, this rule did not predict preferences of mice in habitats with overhead cover, as we suspected (open enclosures: $L=870.5, N=12, NS$; complex enclosures: $L=921, N=12, NS$). However, if nestboxes were ranked first according to accessibility from under the overhead cover, and second according to proximity to the nearest two walls, this matched their preferences between the nestboxes (open enclosures: $L=964, N=12, P<0.01$; complex enclosures: $L=996, N=12, P<0.001$).

### Overall Use of Habitat

Since ground-level complexity and overhead cover strongly influenced both the amount of time that mice spent outside nestboxes (activity) and their use of different sites within the habitat when active, we examined the overall effects of complexity and cover on the total amount of time that mice spent in different sites, whether active or inactive. Figure 8 summarizes the overall pattern of space use. This is subdivided according to the origin of the mice, since mice derived from Nottinghamshire or Cheshire showed differences in general activity in habitats with intermediate levels of structuring (i.e. in open...
ground-level structure with overhead cover or complex ground-level structure with no overhead cover), although origin did not otherwise influence use of space. Despite differences in response to intermediate levels of structuring, site use was similar across all mice when the least (Fig. 8a) or most (Fig. 8d) structured habitats were compared. While mice spent less than a third of their total time outside nestboxes in open habitats with no overhead cover, they spent more than half their time out in habitats that had complex ground-level structure plus overhead cover. Mice also spent much more time both out of nestboxes and away from the enclosure walls when the habitat had a high degree of physical structure (30\% with ground-level complexity and overhead cover compared to 11\% in open habitats with no overhead cover; F_{1,42}=37.64, P<0.0001). In contrast, there was no difference in total time spent close to the two side walls because physical structuring increased the time spent outside nestboxes while decreasing the tendency to stay close to the enclosure walls (Fig. 8a, d).

Figure 7. The nestboxes most preferred (mean rank preference ≥4; black filled circles) and least preferred (mean rank preference ≤2.5; broken circles) by the mice in the eight habitat types. Arrows indicate entrances to nestboxes. In enclosures with complex ground-level structure (e–h), the distribution of bricks was random and differed between enclosures. Predicted order of preference from most to least preferred according to accessibility from under overhead cover (when present) and proximity to two enclosure walls: (a) A>B>D>C>E>F; (b) D>E>F>A>B>C; (c) C>A>F>D>B; (d) F>D>B>C>A>E; (e) A>B>D>C>E>F; (f) D>E>F>A>B>C; (g) C>A>F>D>B; (h) F>D>B>C>A>E.

Figure 8. Percentage of total time spent in different parts of the enclosure according to ground-level complexity (open/complex) and the presence of overhead cover. •: In nestboxes; □: within 12 cm of the side walls; ☐: away from the side walls; □: within the central 16% of the enclosure; ☐: in the area of edge cover.
this central area was still small (1.9 ± 0.3% total time in the least structured rising to 4.5 ± 0.9% in the most structured habitats). Instead, the main effect of physical structure on use of space was to increase time spent in areas that were contiguous to the nestboxes and enclosure walls. In the absence of ground-level complexity and overhead cover, mice spent a high proportion of their time either within the protection of nestboxes or remaining close to the enclosure walls (89 ± 1.8% total time in least structured compared to 70 ± 3.7% in most structured habitats) even though mice were in the dark (recorded under infrared lights). Mice showed intermediate behaviour in habitats with either ground-level structure or overhead cover, Cheshire mice mostly being influenced by ground-level structuring, while Nottinghamshire mice responded to the combined presence of both ground-level structure and overhead cover.

**DISCUSSION**

As we predicted, mice were much less active and more restricted in their use of habitats that had little ground-level structure and no overhead cover, while making much wider use of structurally complex habitats. We found virtually no sex differences in activity or use of space, and behaviour was similar whether mice were active alone or at the same time as their mate. Thus there appeared to be little influence or interference within pairs in their use of different sites. Ground-level structure was clearly the most important of the three factors that we studied, and strongly affected both the time that animals spent outside the physical protection of nest sites and the location of mice that were active. Mice spent a substantial proportion of the dark period outside nest sites only when there was complex ground-level structure (mice spent little time out during the light period, data not presented); this effect on emergence had a substantial influence on the total time spent in different locations (Fig. 8). Apart from nest sites, the outer walls provided the only ground-level structure available in the enclosure. Increasing ground-level complexity in the shape of many small bricks scattered around the floor area promoted considerably wider use of the habitat by increasing the willingness of mice both to emerge from protected nest sites and to move away from the enclosure walls. None the less, even with such complex ground-level structuring, mice still tended to be most active on and around the nest sites and between the nest sites and enclosure walls rather than in the centre of enclosures. Mice also still preferred nest sites and overhead cover that were close to the enclosure walls. This may be because the outer walls provided a continuous line of ground-level structure that mice used as a pathway and that presented an effective barrier to the approach of people or other animals from this direction.

The importance of overhead cover to normal activity depended largely on the presence or absence of complex ground-level structure. The interaction between these two factors was complex since willingness to leave nest sites, and use of the habitat when active, were affected differently by the combination of overhead cover and ground-level complexity. Overhead cover affected where mice went when active only in open habitats, that is, when there was little ground-level structure. Under these circumstances, overhead cover concentrated active mice in sites where there was both overhead cover and at least some ground-level structure in the form of the enclosure walls. Mice could gain direct access to such cover from one or two nestboxes that were also close to the enclosure walls without emerging into an uncovered area. They were not attracted to overhead cover that was surrounded on both sides by uncovered areas with no ground-level structure. Thus, although overhead cover partly compensated for the lack of ground-level complexity in open habitats by reducing the tendency to stay close to enclosure walls, mice still remained in a covered area that was contiguous with enclosure walls and with physically protected resting sites that were close to enclosure walls. Overhead cover was not sufficient to encourage mice to spend more time outside of protected nest sites in the absence of complex ground-level structure. It affected emergence only when there was complex ground-level structure and then only among the Nottinghamshire mice. This might suggest that the Nottinghamshire mice were just more cautious. However, it was the Cheshire mice that spent a greater proportion of time underneath overhead cover when active. The reason for this difference between the two sets of mice is not clear; it could have been caused by subtle rearing or other environmental differences, or by genetic differences according to their origin. None the less, overhead cover affected the location of all mice similarly and it was clear that, while overhead cover added to the effects of ground-level structure in encouraging activity and wider use of the habitat, ground-level structure had the stronger influence.

Although ground-level structure was more important in determining normal activity, mice generally dived under overhead cover sheets in response to an immediate threat from their most common large ‘predator’, a human, and remained there until after the experimenter had gone. Under these circumstances, mice used both central and edge cover, presumably sheltering under the closest cover in the presence of immediate danger. Thus mice were clearly aware that the cover sheets provided protection from large predators. In contrast, ground-level structuring was not considered sufficient protection from large predators since, in the absence of overhead cover, all mice either entered or hid behind a protected nest site: they did not hide within an area of scattered bricks or against an enclosure wall. Overhead cover as well as distance from ground structure (enclosure walls) determined which protected nest sites were normally used.

The limited effects of resource distribution were due to the time that mice spent sitting on top of the nestboxes when active; they spent more than twice as much time here than would be predicted by the size of the area. This behaviour is typical of house mice, which often climb up and sit on top of objects or walls when they are not foraging, moving around or actively defending their territory (Gray et al. 2000; J. L. Hurst, personal observation). This is probably because a higher vantage
point is safer than ground level from the unexpected approach of predators or competitors and nestboxes were higher than the small concrete bricks. Indeed, subordinate males will often shelter in such sites when living in a dominant male’s territory (Crowcroft 1966; Lloyd & Christian 1967); territorial males frequently sit up on raised edges, continually adjusting the angle of each ear while clearly listening for the approach of competitors during territorial disputes, which they then jump on in attack (J. L. Hurst, personal observation). Mice did not otherwise appear to spend more time in the general locality of safe resting sites or near a food dish, and resource distribution did not affect their willingness to emerge from safe resting sites. However, in this study, the area was not large and no location was far from an enclosed resting site or from food. In a less confined situation, nest and food location might have stronger effects on their use of space.

The outsides of nestboxes added to the complexity of the ground-level habitat structure in addition to the physically protected enclosed resting sites inside the boxes. Overhead cover and enclosed sites were clearly the most important habitat features when mice were directly confronted by a human ‘predator’ and seeking safety, so why did ground-level structure have such an important impact on normal activity around the home area? Ground-level structure is likely to be important both for reducing detection and for helping rodents to evade predators or humans once detected. First, staying close to edges is likely to reduce considerably the visual conspicuousness of animals, which are much more visible in the middle of an open area where their outline and movement provide a strong contrast against a simple background than when they are against a more visually complex background with many edges. Although mice are largely nocturnal, humans are their main ‘predators’ in the built environment and their survival is likely to depend strongly on remaining unnoticed. In addition, solid barriers from ground-level upwards reduce the directions from which danger can approach (from any type of predator or conspecific), perhaps explaining why the mice continued to prefer areas near the enclosure walls, even in the presence of complex ground-level structure that they could easily jump over. Similarly, their ability to use raised sites as pathways and when temporarily resting is likely to reduce chance encounters with predators and increase their ability to hear other animals approaching. Perhaps most importantly, animals are considerably harder to catch when there are objects around which they can dodge and hide, particularly when they can move in three rather than two dimensions (J. L. Hurst, personal observation when catching mice in handling bins).

Physical structuring will thus increase the likelihood that animals will be able to evade a pursuer until they reach a site of safety. Physical complexity may also make it much easier to learn and to follow known pathways around the home area and thus to find safety when necessary. Although all mice deposit scent marks around their home area, these are likely to be difficult to follow at high speed in the absence of physical landmarks. Scent marks are not deposited to provide specific pathways (which would also be available to predators) but are deposited on all surfaces visited by the mice (Hurst 1987, 1989). Sites with ground-level complexity are thus likely to offer many benefits and, correspondingly, predation success appears to be reduced in highly complex habitats, although structural complexity can also help to conceal ambush predators (e.g. Mullin et al. 1998).

House mouse habitats in the built environment differ considerably in their physical complexity, from open rooms or grain stores containing few objects, to storage areas, kitchens or intensive farm systems that present a high degree of three-dimensional complexity. From the perspective of controlling mice as pests, it is important to be aware that physical complexity considerably increases the suitability of the habitat for house mice and will allow them to make much wider use of the area. In turn, this will greatly increase the difficulty of applying pest control measures such as baiting or trapping while increasing the number of animals that the habitat is likely to support. Open areas with little ground-level structure will not be very attractive to mice, which are likely to be less active and more confined to physically protected sites within and around the building structure. However, provision of physical shelter such as overhead cover or objects close to side walls is likely to focus mouse activity strongly to these areas in this type of habitat. In contrast, this is not likely to be an effective technique in physically complex areas. However, mice are likely to be more active in such habitats, and control measures could be targeted in preferred sites such as raised pathways and resting sites (identifiable from scent marking). In very complex habitats, odour attractants may be necessary to draw animals to specific sites. However, the most effective and humane form of control would be to reduce physical complexity and thus suitability of the habitat as far as possible, reducing the need for additional mouse control measures.

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