

Microhabitat and spatial dispersion of the grassland mouse (*Mus spretus* Lataste)

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Abstract

Many small mammals inhabiting vegetation habitats where food resources are scattered have large home ranges with limited overlap. One way that they may effectively defend large territories is to establish dominance over the limited number of sites that provide good protection from predators, since displacement from these sites could have a very high cost to intruders. To examine this hypothesis we studied the fine-scale use of habitat and spatial dispersion of all adult male *Mus spretus* inhabiting a 1.1 ha grassland study site near Lisbon, Portugal, by radio telemetry, at the start of the breeding season. The location of each of the 10 males was mapped every hour, 24 h/day for up to seven days. Microhabitat characteristics were compared between a random sample of points in the study site and those where mice were found. Individual ranges did not overlap, despite the close proximity of their borders and the occupation of almost all suitable habitat, suggesting that individual dispersion was strongly influenced by the presence of neighbours; mean range size was $343 \pm 95 \text{ m}^2$. Residents covered less than one-third of their total range over 24 h, though neighbours did not intrude despite the apparent opportunities. Each male territory overlapped the territory of at least two females. Mice were neither nocturnal nor crepuscular, moving around mostly during the morning and evening. They avoided open woodland or pathways, preferring grassland sites with tall vegetation and sites where shrubs, bramble, or dead wood provided additional cover. Most fixes per male (70%) were located in one to four core areas, which represented only a tiny proportion of each range ($6.9 \pm 0.9\%$). Although exclusive defence of large complex ranges is likely to be impracticable, defence of core areas seems much more feasible. Our results thus support our hypothesis that mice may be able to maintain large exclusive ranges due to a combination of high predation pressure and a limited number of sites with sufficient ground and overhead cover. This will result in a very high risk to mice entering areas where competitors have priority of access to protected sites.

Key words: rodents, behaviour, spatial dispersion, territory defence, *Mus spretus*

INTRODUCTION

Although the physical structure of a habitat has received relatively little attention, it is an important factor affecting the social organization of mouse populations, and probably those of other small vertebrates vulnerable to predation. Among other things, physical structuring can affect the ability of mice to exclude conspecifics from their territory, and the degree of contact between neighbouring groups (Barnard, Hurst & Aldhous, 1991). In open habitats with little cover, one male may be able to dominate and aggressively exclude others from large areas (Crowcroft, 1966). More complex areas may be more difficult and costly to defend, since objects

and cover allow intruders to hide and to avoid attack from resident mice (Crowcroft, 1966; Poole & Morgan, 1976). The physical structure of territory borders also affects the ease with which an area can be defended; territories with open borders (those with multiple or unlimited access points) are difficult to patrol, while those with limited access points are easier to defend against intruders (Crowcroft, 1966).

Many mice and other small mammals inhabit grassland and woodland where dense vegetation would seem to provide a structurally complex environment in which intruders could hide. Many studies suggest, however, that under these conditions small mammals often have large ranges of several hundred square metres with limited or no overlap (e.g. Fitzgerald, Karl & Moller, 1981). From a human viewpoint, grassland may seem to be a simple, homogeneous environment, but considered from a rodent's perspective, this is clearly not the case.

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Food supplies are usually scattered over a wide area and, in temperate regions, are seasonal. The density of cover offered by vegetation and tunnel systems, which is important for protecting small rodents from both predators and harsh weather, can also vary considerably over small areas and again changes seasonally. Thus, both habitat quality and suitability are patchy and changeable, and this – combined with competition the mice have from conspecifics and other small mammals that may share their tunnels – makes grassland seem a highly complex environment.

Mus spretus seems to be a typical grassland rodent, inhabiting grass and woodland around the western Mediterranean (Marshall & Sage, 1981). This mouse lives in dense vegetation habitats in which it creates a complex system of interdigitating tunnels through the undergrowth and just under the soil surface (J. L. Hurst, pers. obs.; see also Cassaing & Croset, 1985). These tunnel systems allow the mice to move around the habitat while protected from larger mammal and avian predators, but offer numerous hiding places and points of access for would-be intruders. A trapping study by Cassaing & Croset (1985) indicated that male *M. spretus* occupy large, non-overlapping ranges. This, in conjunction with the high levels of aggression found between males that had been held in isolation in captivity for 3 weeks (Cassaing, 1984), led the authors to suggest that male *M. spretus* patrol large territories, which they maintain by aggressive exclusion of intruders. A more recent study, however, carried out using animals within 1–10 days of their capture (Hurst, Hall *et al.*, 1996) showed that, while competitors exhibit aggressive behaviour, dominant individuals do not attempt to chase subordinate mice away. Subordinates, in turn, do not generally flee from their aggressor but show stylized defensive postures which assuage attack. This competitive behaviour differs significantly from that shown by the more familiar commensal house mouse *M. domesticus* captured from farm buildings (Gray & Hurst, 1997). Territories may be only a few square metres where food resources are concentrated (e.g. Young, Strecker & Emlen, 1950; Crowcroft & Rowe, 1963). Owners quickly encounter intruders and will chase them persistently until they leave the defended territory, while intruders readily flee from such attack. Hurst, Hall *et al.* (1996) suggest that, in contrast, resident *M. spretus* do not attempt to exclude competitors aggressively from their home range area, a strategy which may be impossible to adopt when animals have large, complex ranges.

Trapping data do suggest, however, that *M. spretus* have large, non-overlapping ranges (Cassaing & Croset, 1985; Hurst, Hayden *et al.*, 1994) so, if these are not aggressively defended, how are they maintained? If, in spite of their apparently large ranges, there are only a limited number of safe sites that provide protection from predators, a dominant individual with priority of access to those sites may effectively exclude subordinates without physically forcing them from its entire range.

To obtain the detailed data required to understand how social factors and habitat structure may determine

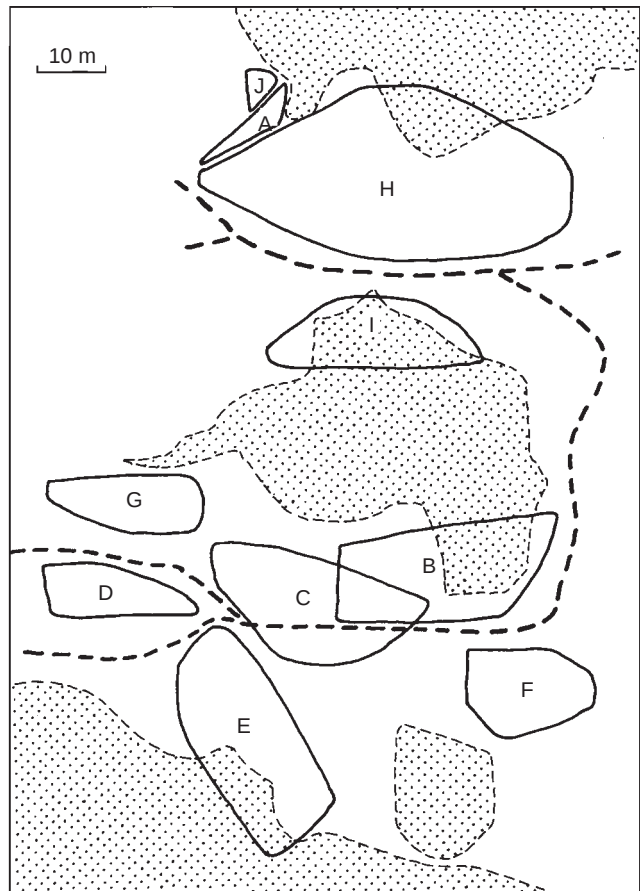


Fig. 1. Map of the study site, showing the distribution of individual ranges for grassland mouse *Mus spretus*. Solid line, 100% convex polygons of each individual's range drawn around the outermost fix points; thick dashed line, pathways; spotted area surrounded by thin dashed line, woodland. Mice were never trapped or tracked in the top left area of the study site; this was an area of scrub with small patches of tussocky grass.

spatial dispersion among male *M. spretus*, we carried out an intensive study of one population using radio telemetry. All 10 adult males using a 1.1 ha site were tracked for up to 10 days to address the following specific questions:

1. How large are individual ranges over the short term and to what extent do they overlap – i.e. are their ranges likely to be defensible and to what extent do neighbours seem to limit an individual's dispersion and access to resources?
2. Do mice use all/most areas within their range or only a limited number of nest and foraging sites that would be relatively easy to defend?
3. Is mouse activity limited to sites with particular habitat characteristics and by the light–dark cycle?

METHODS

The study was carried out near Lisbon, Portugal, between 13 and 23 April 1995. The 1.1 ha study site consisted of mixed dense grassland, woodland, and

Table 1. Number of fixes taken and the area of the range for each mouse

Mouse	Duration of study (days)	No. of fixes	Area of range (m ²)
A	1	23	46.5
B	7	156	396
C	7	158	372
D	3	34	127
E	6	109	424
F	6	119	181
G	6	127	175
H	4	88	924
I	4	74	243
J	4	85	32

small areas of maccacia thicket (see Fig. 1). The dominant shrubs in the grassland were *Inula viscosa* and bramble. The grassland was trapped extensively for a total of 466 trap-nights using Longworth traps containing wheat, peanut butter, and laboratory mouse pellets (Banton & Kingman, Hull, U.K.), with a handful of grass for bedding. The woodland area between the 2 main areas of grassland (see Fig. 1) was also trapped for a total of 54 trap-nights.

All mice caught were sexed, weighed (± 0.25 g), aged as juvenile, subadult or adult (adults classed as those individuals weighing at least 13 g and with adult pelage) and fur-clipped for individual identification. They were housed temporarily in polypropylene cages ($44 \times 26 \times 12$ cm or $30 \times 13 \times 12$ cm) on sawdust substrate with grass for nest material and *ad libitum* food and water. We also trapped a number of shrews (*Crocidura* spp.), which were immediately released at the point of capture.

Radio tracking

All 10 adult males (14–16.5 g) trapped in the study site were fitted with radio-collars to allow us to track their movements simultaneously, sampling their location every hour throughout the 24 h cycle. Since mice were caught, and subsequently released, on different days, the total duration of tracking and number of fix points varied between individuals (see Table 1).

Transmitters (Mariner Radar Ltd, Lowestoft, U.K.) weighing a total of 1.5 g were attached to mice using collars made from nylon cable ties with a non-release ratchet-lock mechanism. After attachment, mice were kept under observation for 2–6 h to ensure they were suffering no ill-effects or loss of mobility, before being released at their site of capture just before dark. Tracking started approximately 2 h after release. Transmitters were located using a TRX-1000S receiver (Wildlife Materials Inc., Illinois, U.S.A.) in conjunction with a hand-held Yagi antenna. Field trials using a transmitter attached to a 'dummy mouse' proved that transmitters could be located accurately to within 50 cm².

The location of each mouse was recorded every hour, 24 h/day, from their release until 20 April (mean $\pm$ SE per male: 4.8 ± 0.61 days). Locations were checked again 2 and 3 days later. In order to minimize disturbance to both the animals and their habitat, established paths were followed as far as possible while tracking. The position of a mouse was recorded in the field by attaching a label onto vegetation over a fix point, giving the date, time and identity of the mouse. The position of each fix point was later recorded onto a detailed and accurate map of the study site, showing areas of the different vegetation types listed below. This allowed locations to be mapped precisely in daylight and minimized disturbance while mice were still in these sites. Once located by tracking, active mice were often observed and seemed to continue moving around normally despite the nearby presence of the tracker. The signal from mouse D was lost after 3 days owing to a faulty transmitter, resulting in a low number of fixes for this individual. Any males detected in traps during radio-tracking were released immediately.

Habitat measures

We recorded the following microhabitat measurements at each fix point:

1. Height of primary vegetation – height from the ground of the highest layer of vegetation over the fix point. This took into account the maximum height of the grass or shrubs over the site being used by the mouse.
2. Height of secondary vegetation – height from the ground of the second highest layer of vegetation over the fix point. This measured the more dense undergrowth through which the mice tunneled.
3. Ground cover – number of grass stems touching the edge of a 10 cm ruler placed at ground level.
4. Presence / absence of shrub or dead wood.
5. General vegetation type – categorized as grass, bramble, shrub, tree, maccacia, geranium or pathway.

The same habitat measures were taken at 2 m intervals along 6 transect lines through the study site (omitting the central woodland), running at right angles to the main pathways, to assess whether there was any bias in the sites used by mice compared to the total area available ($n = 218$ transect points).

Ethical note

The hypothesis tested in this study required detailed data concerning the fine-scale use of the habitat by free-living small mammals, which was not available from previous studies. The reduction of tag size has now made it feasible to radio-track very small mammals, though this may have some energetic costs and perhaps increase their risk of predation. We thus used the minimum number of animals over the minimum time necessary to test our hypothesis, after which we made

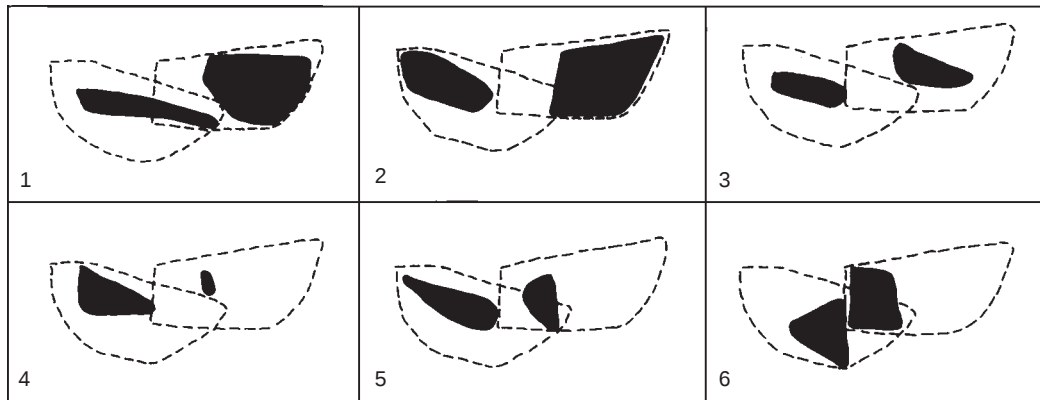


Fig. 2. Daily range (days 1–6) of mice B and C (the two solid areas), shown in relation to their total range (dashed lines). Note that total ranges include data from additional days not shown here. B and C never used the same area over the same time period.

every effort to recapture the mice and remove their collars. Two of the mice were killed by predators (one by a snake, another by a dog) during the study. Six males were re-captured and their collars removed. These animals were used in a further study of their behaviour (unpubl. data) before being released at their capture site.

Data analysis

The location data for the 10 study animals were analysed using Ranges IV software (Kenward 1990). The area map was overlaid with a 1×1 m grid to generate co-ordinates for both fix points and habitat borders. Habitat map co-ordinates were entered to the nearest 10 cm^2 , while fix points could be entered to the nearest square metre. Microhabitat characteristics were compared between fix points (mean per mouse) and transect points by *t*-tests. All results are presented as means ± 1 SE.

RESULTS

A total of 35 mice were caught over 466 trap nights in the grassland areas. Of these, 18 were male (10 adults, six subadults and two juveniles) and 17 were female (12 adults, two subadults and three juveniles). In contrast, no mice were caught in the woodland during the 54 trap nights, set over two nights. This was significantly less than the 20% capture rate found during the first two nights of trapping in the grassland ($\chi^2 = 25$, $P < 0.001$).

Range overlap and size

Figure 1 shows the range of each male represented by 100% convex polygons around their fix points. These polygons were formed by joining together the outermost fix points, thereby encompassing all fixes recorded for an individual (Kenward, 1987). The ranges of individual

males generally did not overlap, even though the borders of several were very close (Fig. 1). Some overlap was apparent between the ranges of males B and C. To see whether these two males used the area of overlap simultaneously, we examined their ranges on each day of the study, but the males were never found in the same area on the same day (see Fig. 2).

There was considerable variability in range size between males ($32\text{--}924 \text{ m}^2$; see Table 1), with a mean range area of $292 \pm 83 \text{ m}^2$ (excluding individuals A and D, for whom we had a very low number of fix points, mean range area = $343 \pm 95.3 \text{ m}^2$). This variation could not be accounted for by the different number of fix points collected for different individuals, since there was no correlation between the two ($r_s = 0.49$, $n = 10$, NS). As we might expect, the mean area covered over 24 h was positively correlated with the total size of an individual's range ($r_s = 0.83$, $n = 9$, $P < 0.025$). We also expected mice with smaller ranges to cover a greater proportion of this area over a given time period, but this was not the case, since the mean proportion of the total range covered in 24 h was not related to the total range size ($r_s = 0.042$, NS; the mean percentage area of range covered in 24 h was $29.5 \pm 3.6\%$). Interestingly, this proportion was remarkably consistent across individuals considering the large differences in range size. Individual ranges seemed to shift to a limited extent over a number of days. For example, this can be seen from the increase in cumulative range area for mice B and C after 6–7 days (Fig. 3), though this did not reflect an increase in their daily range area (Fig. 2). However, when we checked their locations 2 and 3 days after the end of the main tracking period, all mice were still within their previous ranges.

Females seemed to be distributed fairly evenly over the study site, with two to five females trapped within each male range. This represents the minimum number of females overlapping each male since opportunities for females to enter traps were inevitably limited over the short study. Where individuals were repeatedly captured ($n = 9$), female range size seemed to be comparable to males but there was extensive overlap between some

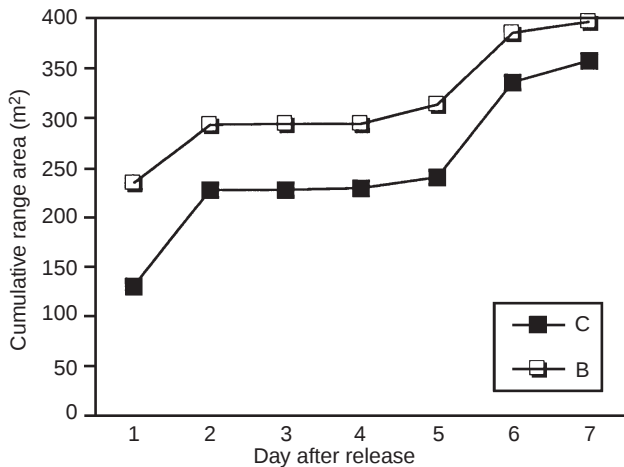


Fig. 3. The increase in total range area of mice B and C as the number of days of tracking increases.

individual females. Similarly to males, females did not seem to cross paths.

Do mice use all areas within a range or a limited number of sites?

To study how mice used different parts of their range we calculated the frequency with which each individual was found within each 1 m² of his range. Figure 4 shows that while some parts of each range were used extensively, many areas were rarely, if ever, visited during the 4–7 day tracking period. Each mouse spent a large proportion of time in only one to four 'core areas', except mouse H who had at least six well-used sites (see Fig. 4). In support of this, a utilization curve (the percentage of fix points plotted against the area of range they occupy; Kenward, 1990) for all mice combined gave an almost horizontal line which only began increasing when 70% of fixes were included. This rise corresponds to the inclusion of excursive activity. This suggests that 70% of fixes occurred within core areas, which represented only a tiny $6.9 \pm 0.85\%$ of each total

range area. In ranges with one core area (males B, E, I, J) these were clearly their nest sites. These data suggest that the core areas of mice C and G (who had two and four core areas within their ranges, respectively; Fig. 4) also represented nest sites where they spent prolonged periods of time, while mice F and H (with four core areas within their range; Fig. 4) seemed to have at least one core nest site and a number of regular feeding sites, which they visited often but not for extended periods. It is important to note that core areas were visited repeatedly throughout the time that mice were tracked; they did not simply represent sites at which mice were inactive at one time over the tracking period. This analysis of the frequency of fixes at each point seemed to be more appropriate for describing their range use than contour analysis (Kenward, 1990), an example of which is shown in Fig. 5 for comparison with Fig. 4B. Contours gave a false impression that all areas within a given contour were visited equally, but clearly this was not the case. Figure 4B reveals that mouse B's core area was found near the edge of his range, while the contour map (Fig. 5) suggests it was much more central.

We tested whether there was any difference in the extent of ranges used during the day and night by comparing the spatial dispersion of their fixes. Dispersion indices were calculated for each mouse's daytime (08:00–21:00) and night-time (22:00–07:00) fix points. This measure of fix dispersion is derived from the minimum harmonic mean distance (which is the sum of the reciprocal distance from each fix to the fix with the shortest mean distance to all others, divided by the number of distances and then re-inverted) divided by its associated standard error (Kenward, 1990). Subsequent analysis of these indices showed no difference in the dispersion of fix points per male during the daytime compared to the night-time (Wilcoxon matched-pair test, $Z = 0.1$, NS).

Are some habitat types used in preference to others?

Mus spretus were restricted to the grassland areas and woodland edges in our study site but avoided open

Table 2. Habitat content of ranges (%R) compared to the habitat at fix points (%F) for each mouse

Mouse	Grass		Wood		Bramble		Path		Geranium		Maccacia	
	%F	(%R)	%F	(%R)	%F	(%R)	%F	(%R)	%F	(%R)	%F	(%R)
A	91	(85)	8.7	(15)	0	(0)	0	(0)	0	(0)	0	(0)
B	92	(67)	5.8	(31)	2.6	(2.4)	0	(0)	0	(0)	0	(0)
C	100	(94)	0	(0)	0	(0.8)	0	(4.9)	0	(0)	0	(0)
D	0	(0)	0	(0)	100	(100)	0	(0)	0	(0)	0	(0)
E	23	(77)	69	(20)	7.4	(1.6)	0	(0)	0	(0)	0	(0.8)
F	100	(100)	0	(0)	0	(0)	0	(0)	0	(0)	0	(0)
G	51	(82)	1.6	(6.8)	47	(12)	0	(0)	0	(0)	0	(0)
H	79	(86)	11	(11)	0	(0)	0	(0)	9.1	(3.9)	0	(0)
I	43	(38)	57	(62)	0	(0)	0	(0)	0	(0)	0	(0)
J	96	(77)	4	(23)	0	(0)	0	(0)	0	(0)	0	(0)
Study site	61.6		28.9		4.7		2.8		1.9		0.1	

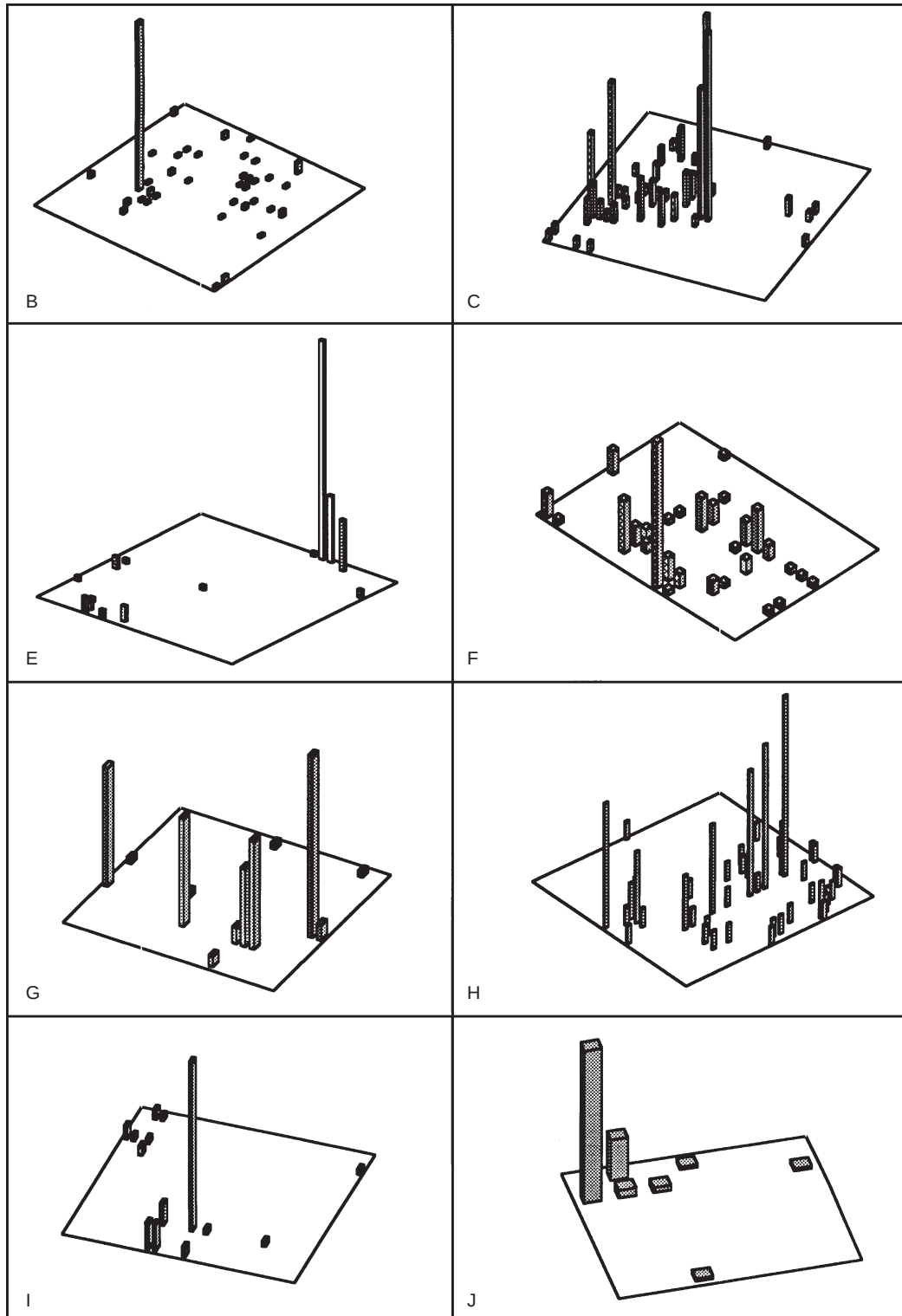


Fig. 4. The distribution of fix points throughout each mouse's range (excluding mice A and D owing to low numbers of fixes). The height of each bar represents the number of times the resident mouse was located within each square metre of its home range, thus the width of each bar represents 1 m.

woodland (Fig. 1). Some individuals nested underground along the edge of woodland (e.g. mice E and I; Table 2), where the much lower density of grass roots may have made it easier to dig shallow burrows, while the mice still emerged directly into the cover of dense

grass when active. *Mus spretus* seemed to use all types of vegetation available as long as these provided sufficient cover. As Table 2 shows, there were large patches of bramble in the study area and, when located within a range, these were used extensively (e.g. mouse G).

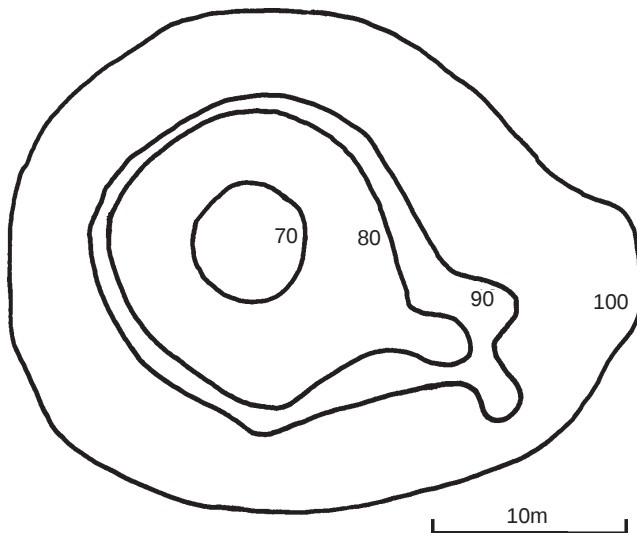


Fig. 5. Contour analysis of the home range of mouse B. Contours show areas of equal fix density, mapped every 10% of fixes.

Similarly, geranium was used when present (mouse H). Grassy pathways, trodden down through the main grassland by human activity, however, were an important habitat feature which seemed to restrict the movement and ranges of mice. The range of most animals bordered at least one pathway (Fig. 1) but, despite this, paths were crossed by only one individual even though they were only 50–150 cm across. Even then, mouse C only crossed a path twice during the seven days (158 fix points) he was tracked. Interestingly the path was particularly narrow (approximately 30 cm) and had dense vegetation overhanging from both sides at the point at which he seemed to cross.

The effects of microhabitat on dispersion

We looked in detail at the microhabitat at points where mice were fixed compared to data from transects taken through the study site. The height of primary vegetation seemed to be an important factor in their choice of location. Mice tended to be found at points with higher primary vegetation than that at random sample points (mean height of primary vegetation at fix points 140.9 ± 29.6 cm; at transect points 85.7 ± 5.9 cm; $t = 1.96$, $P = 0.052$), although there was no difference in the height

of secondary vegetation at fix points ($t = 0.05$, NS). The density of ground cover did not differ between fix and transect points either ($t = 0.83$, NS). This seemed to be because a number of mice nested underground in the edge of woodland or in woodpiles that, despite offering a high degree of cover, did not score on the measure of ground cover used in our study. Mice were much more likely to be found at woody sites within the grassland, i.e. shrubby areas, piles of dead wood, and fallen logs (as distinct from the areas of open woodland), than expected from a random distribution (percentage of points classed as 'woody': mean fix points per mouse 70%; transect points 21%; $\chi^2 = 145$, $P < 0.001$). Although males spent 70% of their time in such sites on average, generally there were only one or two such sites within each range.

Temporal distribution of activity

To investigate whether *M. spretus* showed any circadian pattern in activity, we calculated the mean distance between successive fix points for each mouse through the 24 h cycle. This gave a measure of their active movement (Fig. 6). Mice showed two distinct peaks of activity, but were neither simply nocturnal nor crepuscular; the mean distance moved per hour was high between 08:00 and 10:00, and again between 18:00 and 01:00, and much lower at other times.

The preference for different types of vegetation varied according to whether mice were active or resting. For this analysis, fix points were classed as 'active' if mice had moved location from their previous fix, and 'inactive' if they were still at the same location. When the proportion of fixes in different vegetation types were compared for those mice with more than one habitat type within their range (Table 3), we found that mice spent most of their inactive periods within the habitat type that offered the maximum cover and protection. Where there were patches of dead wood within a range, these were used as resting sites (males E and I), but where there was little wood available, mice rested in patches of dense grass or under the ground (males B, G and H).

DISCUSSION

We found no simultaneous overlap in the short-term ranges of adult male *M. spretus*, despite the proximity

Table 3. Percentage of fix points in each habitat type when mice were active and inactive for those with more than one type of habitat within their range

Mouse	Grass/shrub		Wood		Bramble		Geranium	
	Active	Inactive	Active	Inactive	Active	Inactive	Active	Inactive
B	82.6	97	13	0.9	4.4	2.1	0	0
E	37.5	13.6	43.8	84.7	18.7	1.7	0	0
G	37.5	58.2	2.5	1.3	60	40.5	0	0
H	76.9	93.3	10.8	6.7	0	0	12.3	0
I	73.9	20.5	26.1	79.5	0	0	0	0

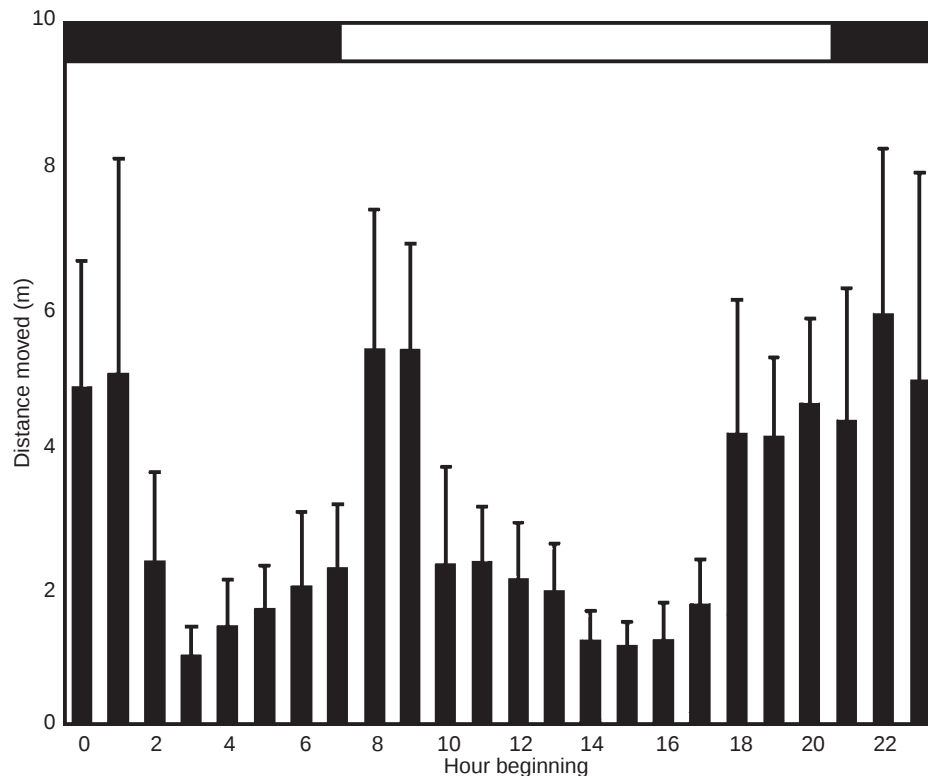


Fig. 6. Distance moved between successive fix points for each hour of the 24 h cycle (mean $\pm$ SE of means per mouse). The light–dark cycle is shown at the top of the graph.

of their borders, confirming previous results from trapping studies (Cassaing & Croset, 1985; Hurst, Hayden *et al.*, 1994). In addition, our results revealed that the 10 males using our study site occupied most of the available habitat (i.e. all areas except the open woodland and pathways). The only area of grassland not used (to the left of mouse E's range in Fig. 1) differed from the rest of the site in that the grass was sparse and flattened, with no matrix of stems to provide covered pathways. Since all areas of apparently suitable habitat were occupied, it is extremely unlikely that the absence of overlap was owing to chance, and it strongly suggests that individual dispersion was determined, at least in part, by the presence of neighbouring males. Although males did not use the same area over the same period, there was evidence for some shift in range size and/or location through time. Cassaing & Croset (1985) also found that the centre of trapping activity within an individual's home range moved by 32–90 m over three months. The range size of the *M. spretus* in our study is comparable with findings from trapping studies. Cassaing & Croset (1985) reported that the maximum distance between recapture sites over a 2 week trapping session was between 13 and 55 m. The maximum width of each of our ranges was within this band, except that of mouse J, whose range was confined to a single woodpile during our study. Ranges were also very similar in size to those of house mice (*M. domesticus*) living ferally in comparable habitats. Male *M. domesticus* inhabiting agricultural fields in southern Queensland were found to have a mean range area of

350 m² when tracked over weekly periods (Krebs, Kenney & Singleton, 1995), which is very similar to the mean of 343 m² we found for *M. spretus*.

The ability of *M. spretus* males to defend the whole of their large range continuously seems unlikely; they did not patrol their entire range, covering less than one third of their total range area in 24 h. In contrast, Fitzgerald *et al.* (1981) found that *M. musculus* inhabiting dense, evergreen forest of New Zealand have even larger exclusive ranges, twice the size of the *M. spretus* ranges reported here, and residents cover most of this area each night. There seemed to be much opportunity among *M. spretus* males for incursion into neighbouring ranges while the resident was elsewhere, so why did this not occur? Our finding that mice were very restricted in the sites that they used, together with the finding of Hurst, Hall *et al.* (1996; see also Hurst, Hayden *et al.*, 1994; Hurst, Gray *et al.*, 1997) that competitors are strongly attracted to such occupied sites, suggests that only a few sites would be attractive to competitors and therefore need to be defended. These 'core areas' were typically small (< 2 m²) and, even when mice had more than one core area within their range, these tended to be close together, and thus still occupied only a small percentage of the total range area. Therefore, although total range areas were large, the most desirable, suitable sites within these ranges were small and clustered together, making defence of these feasible. The characteristic physical nature of these core areas suggested that their attractiveness depended strongly on the protection that they offered. This is not surprising since predation

seemed to be a major threat to survival in our study population. One of our study animals was taken by a grass snake, which was tracked (by the swallowed tag) using the same woodpile previously favoured by its prey, and was later dug out from the mouse's own underground nest. Another study animal was killed by a domestic dog. Owls were also present in the area, which may have added to the predation risk. Although it is possible that the radio collars we attached increased the risk of predation for our males, the frequent presence and behaviour of predators suggested that they regularly caught prey in this site and the surrounding area, and dogs and cats were seen taking animals which were not wearing collars both during the study and in previous years (J. L. Hurst, pers. obs.). Mice caught from another location in a previous study (Hurst, Hayden *et al.*, 1994) favoured sites under gorse bushes (J. L. Hurst, unpubl. data) which, like the bramble bushes in our study site, offer a high degree of protection from larger predators. During other seasons harsh weather conditions are likely to be another important threat to survival, requiring mice to have access to sites that provide adequate protection from the cold and rain, although during our study the weather was warm and dry. Familiarity with an area and the location of proven shelter is probably crucial to survival in such a patchy grassland habitat, while exploring unknown territory could prove fatal. Our data support the hypothesis of Hurst, Hall *et al.* (1996) that mice may thus avoid areas with which they are not very familiar, in favour of known safe sites, especially when they may be displaced by a more dominant male with priority of access to the sheltered sites. Our trapping data show that female ranges overlapped extensively, as has been found in previous studies (Cassaing & Croset, 1985; Hurst, Hayden *et al.*, 1994). Obviously females are also at risk from predation, but familiar animals often show little aggression towards one another and may nest communally and share resting sites, thus removing the need to avoid one another (see Hurst, Gray *et al.*, 1997).

For the first time, our studies have revealed how predation risk interacting with resource distribution and structural complexity may play a major role in determining dispersion and social organization in small mammal populations. This hypothesis leads to a number of testable predictions on the spatial dispersion of small mammals living in vegetation habitats. Where there are few sites providing safe protection from predators, competitors should have non-overlapping, exclusive territories. Where extensive areas of dense cover exist, and for populations exposed to low predation risk, however, the pressure to find covered sites would be greatly reduced. Our hypothesis predicts that under these circumstances exclusive territory defence would be unfeasible, and ranges would then overlap. Ranges are also likely to be smaller as animals would be able to use more feeding sites within their ranges. This is likely to lead to an increase in the density of animals supported by the habitat. We are now carrying out studies to test these predictions.

Unlike many other species of rodent, where light is believed to be the main factor controlling their onset of activity (Montgomery & Gurnell, 1985), *M. spretus* were neither nocturnal nor crepuscular. The temporal pattern of activity in these mice may be related to both predation pressure and ambient temperature. The decrease in mouse activity between 02:00 and 08:00 occurred when the temperature was at its lowest (the temperature in the Lisbon area falls by 7 °C, on average, from its maximum daily temperature to the minimum, which can be as low as 5 °C: Birmingham Meteorological Office, U.K.) and felt appreciably cold to us. Mouse activity was also low between 10:00 and 18:00, when the temperature was at its peak. This also seemed to correspond with the time when snakes were most active. The activity of *M. spretus* was not restricted by light *per se*, probably because their use of tunnels protected them from visual predators such as dogs, cats, and diurnal raptors. This was unlikely to protect them against snakes, however, which hunt at ground level and can infiltrate their tunnel system.

In conclusion, the physical characteristics of the microhabitat had a major effect on the spatial dispersion of individual males, and we suggest that this was largely a result of predation pressure restricting mice to sites that provided sufficient ground and overhead cover. The limited number of such sites, combined with the high level of predation, suggests that access to and familiarity with these sites would be essential. Mice are therefore likely to avoid sites where neighbours dominate and have priority of access, leading to exclusive individual ranges with little or no incursion (Hurst, Hall *et al.*, 1996).

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