Social organization in the aboriginal house mouse, *Mus spretus* Lataste: behavioural mechanisms underlying the spatial dispersion of competitors

JANE L. HURST, SUSAN HALL, RACHEL ROBERTS & CLARE CHRISTIAN

Behaviour & Ecology Research Group, Department of Life Science, University of Nottingham

Abstract. Because rodents behave cryptically and often have large home ranges, the role of social defence in determining their spatial dispersion in grassland remains an enigma. Individual dispersion and access to resources could be determined mainly by the aggressive exclusion of intruders from large territories by residents, or by the scattered distribution of resources and avoidance of dominant competitors occupying preferred sites. The ways in which predictions from these two hypotheses correspond to intra-sexual competitive behaviour within unfamiliar dyads of the mouse *Mus spretus*, recently captured from two grassland populations, were examined. A series of tests in enclosures examined (1) exploration by intruders given a choice between a resident's soiled sites versus clean sites, or between resident-soiled sites versus sites bearing their own odour, in the absence of the resident; (2) the response of an intruder on meeting either the resident or another mouse, in an adjacent clean tunnel; and (3) the response of a resident to an intruder compared with mice meeting in a clean enclosure. In both sexes, dyads quickly established dominance relationships through brief attacks and chases, and static defensive postures, rather than persistent pursuit and flight. Intruders were strongly attracted to a resident's nest and subsequently were more aggressive towards the resident than towards an opponent from an unfamiliar enclosure. There was less differentiation in competitive behaviour and more mutual fighting between residents and intruders than between mice in clean enclosures, with relative body weight being the most important factor determining competitive behaviour. The results were thus more consistent with competition for dominance over suitable sites than investment in fierce aggression to drive competitors away.

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Mark–recapture and tracking studies have revealed a very wide range in home range size, density and spatial overlap between individuals in small mammal populations. House mice (*Mus* spp.) exhibit opposite extremes when they live ferally in grassland on widely scattered food resources, or as commensals of humans exploiting our concentrated resources often within the protection of buildings (Bronson 1979; Berry 1981). It is frequently suggested that the wide dispersion pattern of those using scattered resources is due to extreme intolerance between individuals, with residents fiercely defending their home territory (e.g. Fitzgerald et al. 1981; Mackintosh 1981; Cassaing & Croset 1985). However, it is not possible to infer the behavioural mechanisms

underlying dispersion patterns simply from tracking or trapping data and we do not know what role social defence plays in maintaining the dispersion of rodents in grassland habitats. Exclusive home ranges (e.g. Fitzgerald et al. 1981) could be maintained largely by aggressive defence or by avoidance, both of which can be defined as territorial behaviour (Kaufmann 1983) but would involve very different costs. Similarly, overlapping ranges cannot be interpreted as evidence against territoriality as dominant residents can still be highly intolerant of unfamiliar conspecifics or neighbours intruding into their territory (e.g. Reimer & Petras 1967; Lidicker 1976) or experience differential success in defending particular parts of their ranges (Mares & Lacher 1987).

Ironically, evidence suggesting fierce territorial behaviour comes chiefly from studies of commensal mice defending small home ranges, where interactions between neighbours or between

Correspondence: J. L. Hurst, Department of Life Science, University of Nottingham, University Park, Nottingham NG7 2RD, U.K.

residents and intruders can be observed (e.g. Crowcroft & Rowe 1963; Anderson 1970; Hurst 1986, 1987a). However, such evidence also suggests that commensal mice are unable to defend exclusive territories in large and complex areas where many hiding places allow intruders to evade pursuit by residents (Poole & Morgan 1976; Hurst 1987b), unless access points into the territory are strictly limited (Reimer & Petras 1967) or a large resident family group helps with territory defence (Lidicker 1976). In grassland habitats, where mice may use many inter-digitating tunnels and other runways through the dense undergrowth over comparatively wide areas, the borders of a territory would be open to access at innumerable points. Under these circumstances, there may be little likelihood of an intruder encountering a resident and, even when this happens, intruders should be able to evade a resident without needing to leave the territory. How could rodents defend such large complex areas effectively?

It is often suggested that mammals use scent marks to aid their defence of large territories, serving to advertise their defence even when they are absent from a particular site (see Gosling 1982 for a review). In human environments, the commensal house mouse, *Mus domesticus*, deposits marks extensively (Hurst 1987b, 1989). These are used by males as a cheat-proof advertisement of their ability to dominate a territory; the signal is cheat-proof since only a male that is dominating a site effectively can ensure that his marks predominate on that patch of substrate (Gosling 1982; Hurst 1993). This serves to discourage invasion by mice that have learnt to associate such cues with attack and pursuit (Jones & Nowell 1989; Hurst 1990a, b), discourages challenges for dominance (Gosling & Mackay 1990) and allows mice to take evasive action on meeting the resident dominant (Hurst 1993), thus reducing the costs of territory defence. Such advertisement can be effective even when mice are unfamiliar with the resident (Gosling & Mackay 1990). Mixed cues from more than one male signal that a territory is defended ineffectively, which stimulates attacks against a resident (Hurst 1993).

As yet, it is not known whether such a system could work over very large territories, such as those potentially defended in grassland, if cheats (low-quality competitors or neighbours) could deposit their own marks while a dominant territory owner was elsewhere, or if widely dispersed individuals could lay claim to an unoccupied area without proving their dominance through frequent direct encounters with intruders and neighbours. However, there is some evidence that aboriginal *M. spretus* recently captured from their grassland habitat avoid entering tunnels bearing odours of neighbours though not those of unfamiliar conspecifics, and are defensive in direct encounters after entering a conspecific's tunnel (Hurst et al. 1994).

The nature and extent of agonistic behaviour when individuals meet in different sites, and their use of other social cues such as scent marks or incidental olfactory cues, can tell us a great deal about the nature of their social organization. In this paper we test two alternative hypotheses concerning the social mechanisms that may underlie the spatial dispersion of the aboriginal house mouse *M. spretus*, adapted to living at low density in grassland in regions around the western rim of the Mediterranean (Marshall & Sage 1981). Trapping studies indicate that small groups of mice, generally consisting of a single adult male with one or two adult females, occupy stable, nonoverlapping home ranges of several hundred square metres (Cassaing & Croset 1985; Hurst et al. 1994); this was confirmed recently by a study of 10 neighbouring males that were radio-tracked within an area of approximately 1 ha (J. L. Hurst, unpublished data).

(1) Aggressive exclusion hypothesis. The spatial dispersion of individual mice may be determined largely by the aggressive exclusion of intruders by residents, as in commensal *M. domesticus* populations. This hypothesis predicts that resident territory owners will be highly intolerant and aggressive towards neighbours and unfamiliar intruders, chasing them from the territory. Less able competitors, and those not willing to compete for the territory, should take flight readily and use odour cues to avoid dangerous encounters with residents. Polarity in agonistic encounters will be greater when one competitor is within its own defended territory than when competitors meet on neutral ground. Residents may deposit odour cues around the territory to advertise their presence and reduce the costs of defence. Intruders will use these cues to recognize and flee from a high-quality competitor encountered within its marked territory, and may even avoid entering dangerous areas if the costs are likely to exceed the benefits of intrusion.

(2) Avoidance of dominant competitors hypothesis. The effective exclusion of others from a large territory by aggressive defence may be impracticable when mice are widely dispersed in dense grassland. Under these circumstances, dispersion may be determined largely by the scattered distribution of resources, the difficulty of finding suitable areas that offer sufficient resources and protection (from predators and adverse physical conditions), and the avoidance of high-quality competitors that occupy preferred sites. This hypothesis predicts that resident mice will not try to exclude others from their home range by persistent chasing but will establish dominance relationships during encounters to establish priority of access to preferred sites and mates according to their relative competitive ability. Thus high-quality competitors will be relatively tolerant of the nearby presence of subordinates that immediately submit, while subordinates will show signals of submission rather than rapid flight from the area. Odour cues from conspecifics in the environment will not deter or intimidate unfamiliar intruders as these will not reliably signal a competitor's dominance or the effectiveness of its territory defence. In contrast odour cues, which are likely to be important for orientation in large complex habitats, may be used by others to locate areas suitable for mice and from which they are unlikely to be effectively excluded. Dominance relationships may be territorial (space-related) or absolute (independent of location) (Kaufmann 1983).

We tested these predictions in competitive interactions between both male and female *M. spretus* by conducting a series of tests to examine (1) exploration by an intruder of an occupied (soiled) area in the absence of the resident, (2) the immediate response of an intruder on encountering the resident or another mouse from an unfamiliar area, and (3) competitive behaviour between a resident and intruder compared with mice meeting on neutral (unoccupied) ground. Figure 1 shows schematically the different types of test. All trials involved dyads of unfamiliar mice of the same sex, recently captured from two free-living populations so that our subjects had recent experience of their natural habitat and social relationships.
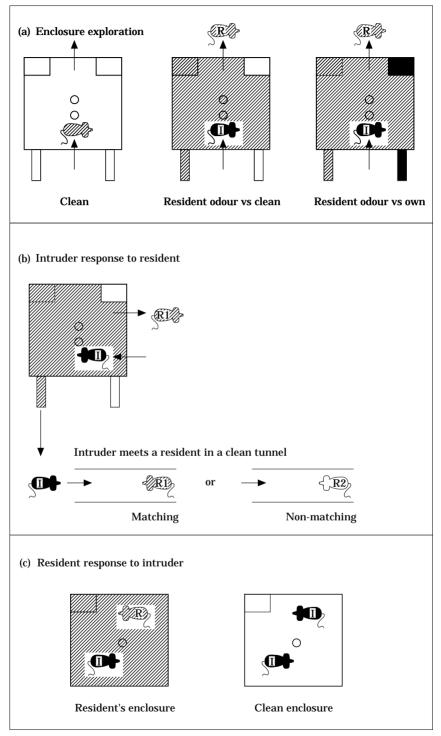
METHODS

The subjects were 20 male and 11 female *M. spretus* caught from two disused farms in Sobreda, Portugal, during April 1993, used in tests 1–8 days after capture. All trials involved single-sex dyads of mice that were caught from different areas (>100 m apart) so that opponents were unlikely to be familiar with each other (see Hurst et al. 1994 for further details of trapping sites). We set 80–120 traps each night for 8 nights, covering eight separate areas. Up to three male and two female adults (weighing at least 12 g, with adult pelage) were caught in any one area; the lack of new adult captures by the end of the study suggested that we caught most of the trappable adults in each site. This was similar to the density and dispersion of mice caught in two previous years in these areas (Hurst et al. 1994). After capture, we weighed the mice and clipped small patches of their dorsal fur for individual identification. The mice were housed singly in cages (30 × 13 × 12 cm) on sawdust substrate with grass for nest material, ample food (laboratory pellets, Banton & Kingman, Hull, and wheat grain) and water. All mice were housed in a darkened room at ambient temperature, where tests were carried out. A small amount of sunlight penetrating the room during the daytime (0730–2130 hours) provided a dim light:dark cycle, supplemented by dim red lighting over the enclosures during the tests.

While all subjects (weight range 7–23.5 g) acted as intruders in the different tests outlined below, only adult mice were used as residents, since only adults were expected to show territorial behaviour. A total of 14 adult males (weight range 12–18 g) and 14 adult females (14–23.5 g) acted as residents. As only nine of the females caught were adult, we had to use five females twice as residents. Six of the females were visibly pregnant and two gave birth and were feeding pups in their home cages during the testing period (all pups survived and were released carefully with their mothers at the end of the tests); pregnant but not lactating females were used as residents in 10 out of 14 replicates.

Establishment of Residents

Between 1700 and 2000 hours each day for 7 days, two male and two female adults were introduced into separate clean enclosures (60 × 60 × 60 cm, varnished plywood) to act as residents in tests conducted the following day. The enclosures contained an open-topped wooden nestbox (15 × 10 × 10 cm), which had an

Figure 1. Scheme of tests carried out to investigate (a) exploration by an intruder (I) of a resident's (R) enclosure, containing a choice of paired nestboxes and tunnels bearing different odours, or of a clean enclosure; (b) the response of an intruder (I) on meeting the resident matching the enclosure explored (R1) or a non-matching resident from another unfamiliar enclosure (R2), in an adjacent clean tunnel; (c) the response of a resident (R) to an intruder (I) compared with intruders meeting in a clean enclosure. ▨: Resident odour; ■: intruder odour; □: no odour.

additional front entrance hole and was filled with dried grass, and two central pots (85 mm diameter) filled with wheat grain and fresh water. Two Perspex tunnels (19 cm long, 3 cm diameter) led out from the side wall opposite the nestbox, one from each half of the enclosure, 42 cm apart. The tunnels were covered with black polythene sleeves, both to encourage entry and to eliminate any differences in lighting that might cause a bias in preference, and their ends were blocked with mesh caps to allow airflow. The nestbox was placed in the left or right hand corner of the enclosure at random to create an odour side for intruder tests (see Fig. 1a and below). A red lamp positioned centrally over the enclosure ensured even illumination and the enclosures were covered with clear plastic glass lids perforated with holes for ventilation.

To avoid stress, we handled all mice by allowing them to enter another clean Perspex tunnel, which they entered readily. Residents were introduced into their enclosure through an entrance hole midway between the two side tunnels which was then closed with a Perspex plug. We recorded their behaviour while exploring the clean enclosure for the first 15 min after introduction for comparison with the behaviour of intruders exploring soiled enclosures (see below).

Residents were left overnight (16–17 h) to establish their odour throughout the enclosure. After establishing the first set of residents in this way, we observed that there appeared to be very few faeces deposited near the nestbox, with most sited near the entrances to the tunnels. As faeces in this species appear to carry information concerning the individual identity of the donor and may be moved to particular sites (Hurst & Smith 1995), we counted the number of faeces deposited overnight on the floor of each quadrant of the enclosure for the remaining 24 residents. Counts were converted to densities to take into account the space occupied by the nestbox. Faeces within the nestbox were not counted, to avoid disturbance, but few if any were found here when the nestboxes were cleaned between trials.

Exploration by Intruders

To assess the effects of an unfamiliar resident's odour on intruder exploration and choice of nest site, we provided intruders with a choice between (1) a nest and tunnel bearing the fresh odours of a resident versus equivalent clean (unoccupied) sites, or (2) a nest and tunnel bearing the fresh odours of a resident versus their own odours, while residents were absent (Fig. 1a). In addition, we measured the same behaviour variables when each resident was introduced into an entirely clean enclosure (see above) to see whether the presence of a conspecific's odour generally increased or decreased exploratory behaviour and whether intruders were willing to enter nests and tunnels.

Residents versus clean sites

Immediately prior to introducing an intruder, we confined the resident in the tunnel opposite its nestbox for 5 min to ensure that both tunnel and nestbox on this side of the enclosure (designated the resident odour side) bore fresh odours from the resident. It was not necessary to hold residents in their nests as they all spent much time there. The tunnel on the other side was replaced with a clean one, and a clean nestbox placed opposite (note that the floor and sides of the enclosure were not cleaned). The resident was then held temporarily in its home cage while an unfamiliar intruder of the same sex was introduced into the enclosure from another clean tunnel. Exploration by the intruder was recorded during its first 15 min in the enclosure. We recorded the frequency of visits to each tunnel and nestbox, frequency of entry, the duration of investigation prior to entry, and any time spent inside a tunnel or nestbox. Investigation was recorded when a mouse's nose was within a tunnel or box (investigation of the outside of the box was not counted), and entry when all four feet were inside. A visit started when the mouse's nose first entered the nestbox or tunnel and ended when the mouse left contact with the box or tunnel. Thus repeated bouts of investigation or entry while the mouse stayed in close contact with a box or tunnel were not recorded as multiple visits. We also recorded the frequency with which the subject's nose crossed a central line drawn on the floor of the enclosure, time spent in each half and the amount of time spent feeding.

As an indication of longer-term preference after this initial investigation, we left the intruder in the resident's enclosure for a further 60 min, recording its location at the end of this period (or, if it was out in the open, its next entrance to a box or tunnel). One intruder was introduced into each

resident's enclosure to give a total of 14 male and 14 female trials, conducted between 1000 and 1200 hours under dim red light.

Resident versus own odour

The exploratory behaviour of intruders provided with a choice between paired nests and tunnels bearing the odours of the resident or their own odour was measured in a similar way, but in this case the intruder was a resident from another enclosure and the soiled nestbox from the intruder's home enclosure was used instead of a clean nestbox (Fig. 1a). Soiled tunnels were obtained by confining both the resident and intruder in clean tunnels for 5 min prior to the trial. At the end of a 15-min trial, intruders were returned to their home enclosures. These trials were not carried out for the first two sets of four residents, giving 10 replicates of each sex for this test. Trials were carried out after the responses of intruders to residents had been recorded (see Fig. 1b and below) and residents had settled back in their home enclosures for at least 3 h.

Response of Intruder to Resident

To assess whether intruders use odour cues in the environment to identify an unfamiliar resident and alter their behaviour accordingly when they meet, we had to eliminate any effects that surrounding odours might have on the behaviour of their opponent. Intruders were thus allowed to explore a resident's enclosure and then, on leaving the resident's tunnel, they immediately encountered either the matching resident from that enclosure, or a non-matching resident from a different enclosure, in a clean tunnel (Fig. 1b).

This test was conducted using the intruders and residents from the intruder exploration trials detailed above (resident odour versus clean trials only), immediately after intruders had explored the enclosure of a same-sex resident for 75 min. Half the intruders were allowed to meet the resident from the enclosure they had just explored (Matching trials, $N=14$) while the rest met a resident from an enclosure that they had not explored (Non-matching trials, $N=14$). Encounters took place in a clean tunnel (38 cm long, 3 cm diameter) but the intruder was first confined for 3 min in the resident-soiled tunnel, and introduced from here, so that it experienced the encounter

within an area otherwise suffused with the resident's odour. A matching or non-matching resident was settled at one end of the clean tunnel (facing inwards) and the intruder introduced from the opposite end, ensuring that the resident opponent had no contact with the soiled tunnel. The mice were then sealed in the clean tunnel by mesh caps and their behaviour recorded for 5 min by two observers and a recorder. The short duration of this test was designed to measure the initial response of the intruder, potentially primed by its recent experience. We recorded the frequency and duration of encounters when a mouse's nose was within 3 cm of its opponent together with the frequency of occurrence of any of the following social behaviour patterns, for both intruder and resident: approach (moving to within 3 cm of opponent), retreat (backing or turning away from opponent), investigation (sniffing any part of the body), nose up (nose held at or above the horizontal), squeak, eyes closed, push (trying to push past the opponent with their nose), shove (pushing the opponent away with one or both forepaws), attack (a bite or rapid scrabbling with forepaws), and sit by (stationary within 3 cm of opponent, showing none of the directed behaviour patterns listed above for at least 20 s). The diameter of the tunnel was such that mice could just turn around but found it very difficult to push past each other. Mice passed each other in only three trials.

At the end of a trial, the intruder was returned to its home cage and the resident returned to its home enclosure with its original nestbox. The clean nestbox and both tunnels were removed and the resident allowed to settle for at least 3 h before the next type of test. To ensure that there were no temporal effects, we conducted replicate Matching and Non-matching trials on alternate days, with opposite alternation for males and females.

Ethical note

Pilot tests and an experiment conducted the previous year (unpublished data, 108 dyadic pairings) showed that aggression never escalated to more than a few brief attacks in these narrow tunnels, providing us with the opportunity to investigate defensive behaviour (and aggressive challenge) that was not stimulated by an immediate attack when the intruder encountered another mouse. We were prepared to separate dyads if there was persistent biting or desperate attempts

to escape, but this did not occur. Aggression occurred in 39% of trials, with a maximum of five bites or 10 scrabbling attacks in any one trial.

Response of Resident to Intruder

To assess whether residents attempt to defend their enclosure aggressively against intruders, and to examine the nature of agonistic behaviour in this species, we introduced an unfamiliar same-sex intruder into each enclosure while the resident was present. This was compared with behaviour when two intruders met in an identical neutral (clean) enclosure to assess (1) the importance of body size in determining relative competitive ability, and (2) whether prior residence and resident odours affected agonistic interactions between the mice (Fig. 1c).

Resident response to intruder trials were conducted after mice had been resident for 21–24 h (pilot tests with *M. domesticus* indicated that this was sufficient time for resident commensal mice to show territorial defence). An unfamiliar same-sex intruder was introduced into each resident's enclosure from a clean tunnel inserted in the side wall. The entrance hole was plugged and all interactions occurring over a 10-min period were recorded by two observers and a recorder. As residents were often resting in the nestbox at the start of a trial, the recording period did not start until the first encounter between the two mice. In contrast to behaviour in the tunnels where mice were closely confined together, mice in enclosures interacted in a number of clearly separated encounters. We recorded the frequency and duration of each separate encounter, defined as starting when one or both mice approached to within 3 cm of each other and ending when the mice separated and showed no directed attention towards each other. We also recorded whether any of the following behaviour patterns were shown during an encounter by the resident or intruder: approach, retreat or flee, close investigation (nose within 3 cm or touching opponent), distant investigation (sniffing towards with nose more than 3 cm from opponent), defend (reared up on back feet or rolled over onto back or side with nose raised above the horizontal, usually with forepaws up and outstretched), shove (pushing opponent away with forepaws or kicking with hind foot, usually while defending), squeak, attack (sudden lunge at opponent), chase (rapid

pursuit of opponent), fight (mutual wrestling or scrabbling with forepaws), allogroom (grooming the fur of opponent) and sit by (resting within 3 cm of opponent while showing none of the above for at least 20 s). Multiple occurrences of a behaviour during the same encounter were scored only once.

At the end of a trial, both intruder and resident were returned to their home cages and the enclosure thoroughly cleaned with detergent and wiped with alcohol, in preparation for the introduction of a new resident. One trial was conducted per resident, giving a total of 14 male and 14 female trials.

To test equivalent dyadic behaviour in a neutral area, we introduced two unfamiliar same-sex mice into an equivalent clean enclosure containing a clean nestbox, food and water pots, and recorded their interactions for 10 min from first encounter as above. Individual mice were used in resident and neutral enclosure trials on different days, and they always encountered different opponents. Since it was essential to test dyads that had not met previously in other tests and that were caught from different sites, we could conduct only 13 male and five female neutral area trials using the mice caught in this study. Caution thus needs to be shown in interpreting the generality of female behaviour from such a small sample size.

Ethical note

As mice might show extensive aggression in these trials, especially if residents were stimulated to exclude other mice from their territory, we decided to separate any dyads showing persistent aggression such as extensive chasing or biting. However, as will become apparent from our results, the mice did not show such intolerance and no trials were curtailed. Aggression occurred in 81% of resident and 94% of neutral enclosure trials, with 3.6 ± 0.6 ($\bar{X} \pm \text{SE}$) encounters involving aggression per trial, mostly involving a brief attack (total number of encounters per trial $\pm$ SE was 9.7 ± 0.6). We did not time the duration of aggression per se, but the total duration of encounters that involved aggression $\pm$ SE was 5.3 ± 0.4 s, excluding those in which the mice ended up sitting together. Attacks and chases at the start of a trial (chasing occurred in 38.5% of aggressive encounters) quickly resolved to one mouse showing defensive postures, often the one

that initiated the encounter, while the aggressor sniffed and retreated.

Data Analysis

For the intruder exploration tests, we used non-parametric Wilcoxon matched-pair tests to examine the significance of any bias in intruder behaviour towards (1) resident odour versus clean sites, and (2) resident versus own odours (using the normal deviate approximation for large sample sizes except when $N < 20$). We used parametric t-tests to check for sex differences in the bias shown towards (resident − clean) or (resident − own), and for any difference in bias between these two different types of choice (difference scores closely approximated normality). We compared intruder exploration in the resident odour versus clean choice test with exploration when residents were first introduced into a clean enclosure using non-parametric Mann–Whitney U-tests. All significance tests were two-tailed.

For each test involving social interaction, we used principal component analysis (PCA) to summarize the main behaviour patterns shown by individual mice or dyads, based on log transformations of their total score per trial for each type of behaviour recorded. Principal component analysis was carried out on the correlation matrix (i.e. using standardized variables with zero means and unit variances) to ensure that all variables had equal weight in the analysis. We then examined the weights applied to the behavioural variables for the first six derived components of each PCA to identify those components that described behavioural patterns of relevance to the predictions under test. We used matched-pair t-tests and parametric ANOVAs to examine the effects of status and sex on the derived PCA scores, all of which closely approximated normality, and Pearson correlations and matched-pair t-tests to examine the effect of size difference within dyads. All significance tests were two-tailed, since the two hypotheses often had opposing predictions, except for those concerning the effects of relative size; these tested the prediction that the heavier mouse would be more aggressive and less defensive than its lighter opponent, since the heavier animal usually dominates when *M. domesticus* (Barnett et al. 1980; van Zegeren 1980) and many other rodent species (e.g. Grant 1970) meet on neutral ground.

RESULTS

Exploration by Intruders

When exploring a resident's enclosure, intruders did not avoid the resident's odours but, on average, spent twice as much time in the side of the enclosure that contained the soiled nest and tunnel as in that containing clean sites (Table I). There was no sex difference in this bias which was due entirely to the intruders' response to the soiled and clean nest sites, not to their response to the tunnels (see Table I). Mice of both sexes showed an overwhelming preference for the soiled nest, with only two of 28 mice spending more time in the clean nest. Intruders both visited and entered the soiled nest more frequently, and also stayed longer each time they entered the nest. The only significant sex difference in behaviour was due to males visiting and entering the soiled nest more frequently than females did (Table I). Both male and female intruders thus spent more time within a nest soiled by a same-sex conspecific than in an equivalent clean nest, while males were also stimulated to visit the nest repeatedly. After a further hour in the enclosure, intruders still tended to be found within the side containing the soiled nest and tunnel (in 15 of 25 trials where location was recorded) but this bias was not significant (binomial test: $z = 0.80$, NS).

When intruders were provided with a choice of the resident's or their own nest and tunnel, they still tended to spend more time in the side containing the resident-soiled sites, although in this case the overall bias towards the resident odour side was not significant (Table I). Intruders of both sexes visited and entered the resident's nest more frequently than their own (Table I), and spent longer sniffing into this nest from the outside ($z = 2.82$, $P < 0.005$). However, while males also spent more time inside the resident's nest ($W = 4$, $N = 10$, $P < 0.05$), females showed significantly less bias in entry (Table I) and failed to spend more time in the resident's nest than within their own ($W = 25$, $N = 10$, NS). Thus, male intruders spent more time in a resident's nest regardless of the alternative (difference in bias between the two different choice tests, $t = 0.24$, $df = 22$, NS) while female intruders showed a preference only when the alternative was a clean nest not their own ($t = 2.76$, $df = 22$, $P = 0.01$).

Table I. Exploration by intruders

	Odour choice $\bar{X} \pm$ SE		Bias		Sex difference	
	Resident	Clean	z†	P	t‡	P
Time in each side (s)	591 ± 40	295 ± 40	3.15	***	1.17	NS
Response to nests						
Time inside (s)	289 ± 36	35 ± 10	4.29	****	1.02	NS
Visits	8.8 ± 0.8	5.5 ± 0.7	2.60	***	2.57	*
Entries	7.4 ± 0.8	3.4 ± 0.6	3.68	****	3.44	***
Duration per entry (s)	46 ± 6.7	11 ± 2.1	3.99	****	− 2.05	NS
Response to tunnels						
Time inside (s)	76 ± 34	59 ± 32	1.57	NS	0	NS
Visits	6.0 ± 0.7	5.3 ± 0.7	1.46	NS	− 0.69	NS
Entries	2.7 ± 0.5	1.9 ± 0.3	1.15	NS	− 0.38	NS
Duration per entry (s)	55 ± 38	52 ± 38	1.36	NS	0.14	NS
	Resident	Own				
Time in each side (s)	526 ± 64	336 ± 62	1.40	NS	1.68	NS
Response to nests						
Time inside (s)	205 ± 48	108 ± 52	1.71	NS	2.32	*
Visits	5.0 ± 0.7	2.7 ± 0.4	2.61	**	1.54	NS
Entries	4.0 ± 0.7	1.6 ± 0.4	2.87	***	2.10	*
Duration per entry (s)	52 ± 12	72 ± 44	1.19	NS	1.66	NS
Response to tunnels						
Time inside (s)	132 ± 52	91 ± 47	1.55	NS	− 0.26	NS
Visits	5.7 ± 1.1	4.6 ± 0.8	1.49	NS	− 0.61	NS
Entries	2.9 ± 0.6	2.1 ± 0.5	1.65	NS	− 0.60	NS
Duration per entry (s)	72 ± 42	56 ± 39	1.74	NS	0.46	NS

†Wilcoxon matched-pair test for both sexes combined.
‡*t*-test of difference in bias (resident − clean) or (resident − own) between males and females.
*$P<0.05$; **$P<0.01$; ***$P<0.005$; ****$P<0.001$.

The presence of a resident's odour within the enclosure had little general effect on the exploratory activity of intruders: there were no differences in tunnel exploration, feeding or crossing the central line compared with mice exploring a clean enclosure. Substrate odours specifically increased the frequency of entry ($z= − 3.24$, $P<0.005$) and time spent within ($z= − 2.63$, $P<0.01$) a resident's nest compared with a mouse investigating a clean enclosure and nest site.

Faecal Distribution

The distribution of faeces deposited by individual residents of both sexes was highly consistent, confirming a strong bias in faeces being located near the tunnels and away from the nestbox (Table II), although the numbers deposited varied greatly (range overnight 26–211 per individual). We ranked the number dropped in each

Table II. Percentage ($\bar{X} \pm$ SE) of faeces deposited overnight by residents in different quadrants of their enclosure

	Males	Females
Nest	13.2 ± 1.6	10.9 ± 2.0
No nest or tunnel	16.0 ± 1.8	12.4 ± 2.6
By nest and tunnel	31.6 ± 4.3	36.4 ± 2.8
By tunnel only	39.2 ± 2.9	40.3 ± 3.7

quadrant of the enclosure from the lowest (1) to highest (4) density for each resident and then used a Meddis non-parametric analysis for related samples (Meddis 1984) to confirm that fewer faeces were deposited on the side of the enclosure containing the nestbox (specific test, $z=1.90$, $P<0.05$); the location of the tunnels, however, was the main factor influencing distribution with most

faeces deposited in the two quadrants that led to the tunnels (specific test, $z=7.95$, $P<0.0001$).

Response of Intruder to Resident

Within the confines of a narrow tunnel, the mice approached and investigated each other and often tried to push past, usually without success. Defensive behaviour was very common in tunnel interactions, shown by at least one of the mice in most (24/28) trials. This involved a mouse raising its nose to the horizontal, often with eyes closed, and sometimes squeaking; an opponent trying to investigate or push past was often shoved back with one or both forepaws. Lunging attacks were very rare and no chases or fights were observed, but one mouse sometimes bit or scrabbled at the other while in close contact, especially when being pushed by the other mouse.

Three factors were likely to have important effects on the behaviour of intruders: the apparent status of their opponent (the resident matching the enclosure they had explored or a non-matching mouse), the sex of the dyad, and the size difference between intruder and opponent. The main behaviour patterns of individual mice within tunnels were summarized quantitatively by principal component analysis of both the intruder and opponent responses per trial ($N=56$). We examined the effects of apparent opponent status and dyad sex on the derived scores of intruders using two-way analysis of variance and correlated differences in those behaviour patterns within a dyad with the weight difference between the mice.

The first two derived components reflected general levels of activity shown by the mice (moving along the tunnel and the total amount of defensive and aggressive behaviour), which accounted for most of the variability in behaviour between individuals (54%). Intruders showed no significant difference in either type of activity on meeting a matching or non-matching opponent, and there were no effects of dyad sex.

An intruder's willingness to challenge when encountering a matching resident or a non-matching mouse was shown by the fourth principal component (accounting for 9.3% of the total variance). This contrasted aggression and, to a lesser extent, push and retreat with sitting next to, sniffing, squeaking and shoving the other mouse away with the forepaws. In contrast to the prediction that intruders would be less likely to challenge a matching resident (aggressive exclusion hypothesis), intruders were more likely to be aggressive and less likely to sit by and show defensive behaviour towards a matching resident than towards a non-matching mouse whose odour they had not encountered in the environment (effect of opponent status, $F_{1,24}=4.45$, $P<0.05$, with no significant effect of dyad sex, $F_{1,24}=0.12$, NS or interaction between sex and status, $F_{1,24}=0.17$, NS). It is possible that this increased aggression and reduced affiliation towards matching residents was induced by information gained from odours in the enclosure which indicated that some residents were of low competitive ability. As competitive ability was likely to depend on weight (see below), we tested whether intruder scores for this component were related to the weight of the matching resident ($r=0.27$, $N=14$, NS) or to the weight difference between intruder and resident ($r=-0.09$, $N=14$, NS). Although neither correlation was significant, it should be noted that intruder scores (and hence aggression) tended to increase rather than decrease with the weight of a resident opponent.

The only other pattern of behaviour that involved aggression (third component, 12.4% variance) occurred when one member of a dyad was trapped, usually at the end of the tunnel, by its opponent sitting next to it and blocking the way. When the trapped mouse attempted to push past, the blocking mouse often bit or scratched causing the trapped individual to squeak and attempt to withdraw. Such aggression was not sustained, and occurred only when provoked by pushing. Intruders did not discriminate between matching or non-matching opponents with respect to this behaviour ($F_{1,24}=0.004$, NS) and there was no effect of dyad sex ($F_{1,24}=0.53$, NS). Not surprisingly, there was a strong relationship between the weight difference of mice in a dyad and their scores for this component ($r=0.54$, $N=28$, $P<0.005$), with the larger mouse showing relatively more blocking behaviour and the smaller mouse more pushing and squeaking, regardless of their intruder/opponent status.

Analyses of variance confirmed that the opponent's behaviour towards an intruder did not differ according to the opponent's apparent residence status for any component scores (such differences might have been induced if a resident had detected its own odour contaminating the body of the intruder), thus the difference in

intruder behaviour towards matching and non-matching opponents was due only to the behaviour of the intruder. Neither opponent status nor dyad sex had any significant effects on the total contact time or frequency of encounters within the tunnels (though note that intruders had less control over contact within tunnels than in more open areas).

Neutral Area Interactions

To assess how the size difference between mice affected their competitive interactions in open areas, we derived the main patterns of behaviour shown by individual mice in dyadic encounters in a neutral (clean) enclosure by principal component analysis, and compared component scores between the larger and smaller mouse of each dyad.

A large proportion (43%) of the variance in behaviour was accounted for by the first component derived, which contrasted the active initiation of interactions and aggression (positive weight given to approach, attack, investigation and chase) with defensive behaviour (negative weights for defend, squeak, shove and retreat). As expected, the larger mouse showed more aggressive and less defensive behaviour than the smaller (matched-pair t-test of component scores: $t=2.38$, $df=17$, $P<0.02$) with no sex difference in this bias ($t=-1.54$, $df=16$, NS). The difference between the two mice increased with increasing difference in their size ($r=0.47$, $N=18$, $P<0.05$). Other derived components contrasted general levels of agonistic behaviour (aggression and defence) with avoidance (retreat and distant investigation) between the mice (11% of variance), and interactions involving differing degrees of physical contact (17% of variance), which necessarily were similar for both members of a dyad.

Response of Resident to Intruders

We compared resident and intruder behaviour patterns by matched-pair t-tests of their scores derived from a principal component analysis of individual behaviour in trials where one individual was a prior resident in the enclosure. The influence of the relative body size of the two mice was examined by correlating the difference in resident and intruder scores with the difference in their weights. As some trials were conducted using juvenile intruders (all residents were adults) and

weight was an important component determining social response, we used data only from trials in which intruders were of the same minimum weight as residents (at least 12 g, $N=21$) to assess the effects of prior residence on behaviour and checked that there was no difference in the mean weight of residents ($\bar{X}\pm$ SE$=16.9\pm0.6$ g) and intruders (16.9 ± 0.6 g) in these trials.

Scores for the first two derived components (44.8% of variance in behaviour) were related to the weight difference between the mice but did not differ according to their prior residence status, while the third component (17.5% of variance) differed strongly according to their residence status but was independent of relative body size. The first component was similar to that derived from interactions in a neutral area, contrasting approach and aggressive behaviour with stationary defensive behaviour, although not in this case with retreat (Table III). As in neutral areas, the difference in scores within a dyad depended on the difference in their weight such that the larger mouse showed relatively more aggressive and less defensive behaviour than its smaller opponent ($r=0.45$, $N=28$, $P<0.01$). When mice were of similar size, however, the difference in their scores covered a wide range (Fig. 2a). Note that there was no difference in the scores of residents and intruders for this component ($t=-0.41$, $df=20$, NS) despite the fact that scores represented a clear comparison between aggression and defence, with no sex difference in this lack of bias ($t=-0.28$, $df=19$, NS).

The second component contrasted agonistic (defensive and aggressive) with non-agonistic behaviour (sit by, allogroom and social investigation), reflecting the fact that mice did not show agonistic behaviour in all trials. Not surprisingly, there was no difference between resident and intruder scores within each dyad ($t=1.12$, $df=20$, NS) as there was a strong correlation between their scores, both or neither mouse showing agonistic behaviour ($r=0.60$, $N=22$, $P<0.005$). However, the difference in their scores was negatively related to the weight difference between the mice ($r=-0.41$, $N=28$, $P<0.05$ for two-tailed test since the effect of size was not clearly predictable in this case). When one mouse was much larger than the other, the larger individual showed less agonistic (especially defensive) and more non-agonistic behaviour relative to the smaller mouse; either mouse showed the higher score

Table III. Principal component weights describing behaviour of mice in resident enclosures

Behaviour	Principal component				Behaviour scores*	
	1	2	3	4	Resident	Intruder
% Variance	25.3	19.5	17.5	9.4		
Approach	0.43	− 0.05	− 0.33	0.12	2.9 ± 0.6	5.0 ± 0.7
Retreat	0.15	0.12	− 0.60	− 0.08	2.2 ± 0.4	5.7 ± 0.7
Investigate	0.17	− 0.23	− 0.45	0.08	3.8 ± 0.6	4.7 ± 0.6
Sniff towards	0.21	0.29	− 0.07	− 0.51	1.0 ± 0.3	0.7 ± 0.2
Defend	− 0.39	0.34	− 0.21	0.00	1.7 ± 0.5	2.1 ± 0.4
Shove	− 0.36	0.14	0.07	0.51	0.6 ± 0.2	0.5 ± 0.2
Attack	0.35	0.28	0.36	0.05	2.4 ± 0.6	1.0 ± 0.4
Chase	0.42	0.19	0.25	0.20	0.9 ± 0.3	0.4 ± 0.2
Fight	− 0.01	0.29	0.14	− 0.39	0.4 ± 0.2	0.3 ± 0.1
Squeak	− 0.31	0.44	− 0.19	− 0.15	0.9 ± 0.3	1.6 ± 0.4
Sit by	− 0.17	− 0.42	0.01	− 0.15	1.3 ± 0.3	1.2 ± 0.3
Allogroom	− 0.13	− 0.37	0.18	− 0.47	0.2 ± 0.1	0.2 ± 0.1

*Mean ± SE of interactions in which behaviour was shown. There were 8.3 ± 0.8 interactions per trial.
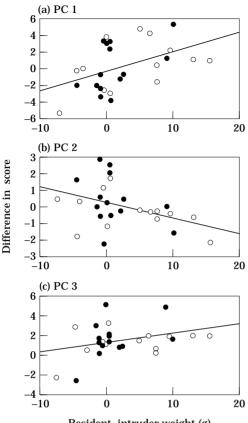
when the mice were of similar size (Fig. 2b). This was due largely to the high frequency of squeak and defensive posture shown when a mouse encountered a much larger one, regardless of any aggression.

The third component was a strong contrast of unidirectional aggressive behaviour (attack and chase) with retreat and approach (ending and initiating interactions), social investigation and, to a lesser extent, defensive postures and squeaking (Table III). There was a highly significant difference in the scores of residents and intruders for this behaviour pattern ($t=3.69$, $df=20$, $P<0.001$), with no sex difference in the bias ($t=0.25$, $df=$ 19, NS). Residents showed more aggression and much less retreat from interactions as expected, but they also tended to initiate fewer interactions and show less social investigation than intruders. Despite aggression from residents (which usually was very brief) followed by the retreat of the intruder, intruders continued to approach and investigate the resident. Residents showed higher scores than intruders for this component in almost all trials, except for two cases in which the intruder was more than 4 g heavier than the resident (Fig. 2c). Note that this investigation and retreat response of intruders to resident aggression differed from the agonistic behaviour represented by component 1 (above), which showed that lighter

mice were consistently defensive towards a heavier aggressor but were not more likely to retreat.

Scores for the fourth component did not differ between residents and intruders but represented an interesting contrast between shove behaviour, which occurred mostly when there was little or no weight difference between the two mice (Fig. 3), and other behaviour (distant investigation, such as sniff towards, allogroom and fight) which tended to occur when there was a large difference in size between the mice. In open areas, shove was shown when mice already in a defensive posture put up their forepaws to push away the other mouse which might be investigating, threatening or attempting to attack.

Residents tended to be the first to initiate aggression in a trial as expected by both hypotheses (resident initiated first in 12 trials, intruder in five trials when the intruder was at least 12 g; binomial test: $z=1.46$, one-tailed $P=0.08$) though by the end of a trial residents clearly dominated in only 10 trials and intruders in six ($z=0.75$, one-tailed $P=0.23$) suggesting that prior residence did not secure dominance. Greater size did not determine dominance either (eight larger and six smaller mice clearly dominated with respect to aggressive behaviour) but in five of the six cases when the intruder dominated, this was the larger of the two mice.

Figure 2. Effect of the weight difference between residents and intruders meeting in the resident's enclosure on the difference in their scores for the main patterns of behaviour derived by principal component analysis (weights applied to each behaviour given in Table III). ○: Females; ●: males. (a) Approach and unidirectional aggression contrasted with stationary defence (component 1). (b) Agonistic (squeak, defend, fight, towards, attack) versus non-agonistic (sit by, allogroom, investigate) behaviour (component 2). (c) Aggression (attack, chase) contrasted with movement (approach, retreat), investigation and defend (component 3).

Behaviour in Neutral versus Resident Enclosures

Data from neutral and resident enclosure trials were combined to allow direct comparison of behaviour in these two situations. We used two-way ANOVAs to examine the effects of enclosure type and dyad sex on the number and duration of interactions. There were more interactions per trial when mice met in a neutral area (neutral: $\bar{X} \pm \text{SE} = 11.9 \pm 0.8$; resident: 8.3 ± 0.8; $F_{1,41} = 11.0$,
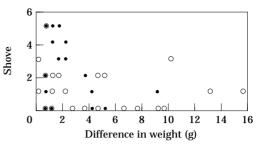

Figure 3. Number of encounters per trial involving shove behaviour according to the absolute difference in weight within a dyad ($r = -0.33$, $N = 46$, $P < 0.05$). ○: Resident enclosures; ●: neutral enclosures.

$P < 0.005$), but the total duration of interactive behaviour was greater in resident enclosures ($F_{1,41} = 5.7$, $P < 0.05$) since the mean duration of each interaction was much greater (neutral: $\bar{X} \pm \text{SE} = 11 \pm 2$ s; resident: 53 ± 14 s; $F_{1,41} = 5.8$, $P < 0.05$). We examined whether this was due to a difference in the location of interactions, since mice meeting in the nestbox often tended to stay near each other, but there was no difference in the proportion of interactions per trial occurring in the nest ($F_{1,41} = 1.46$, NS). Gender had no significant effect on any aspects of behaviour.

A principal component analysis based on the total behaviour of both members of the dyad allowed us to compare overall levels of different social behaviour between these two situations (component weights are given in Table IV). Mice in neutral areas showed more social behaviour involving active movement (retreat, approach, aggression, defence and investigation) and less stationary affiliative behaviour (sit by, allogroom) (component 1 explaining 35% of variance, $F_{1,41} = 10.3$, $P < 0.005$). In contrast, when meeting within an area already occupied by one of the opponents, the mice showed more aggression relative to neutral investigatory, approach, retreat and shove behaviour (component 3, $F_{1,41} = 6.4$, $P < 0.05$) and more fighting and chasing relative to distant investigation (component 6, $F_{1,41} = 6.3$, $P < 0.05$).

To assess whether there was greater differentiation in competitive behaviour between the mice in these two situations, we used a second analysis to compare the absolute difference in individual scores based on the individual behaviour patterns of the mice. Greater differentiation was found with respect to scores for the first derived

Table IV. Principal component weights describing total dyadic behaviour of mice in resident and neutral enclosures

	Principal component						Behaviour scores* per dyad	
	1	2	3	4	5	6	Resident	Neutral
% Variance	35.1	16.8	15.6	9.3	6.6	5.5		
Approach	0.39	0.15	− 0.34	0.11	0.09	0.09	7.9 ± 0.8	12.0 ± 0.9
Retreat	0.41	0.17	− 0.28	0.17	0.07	0.11	7.9 ± 0.8	12.1 ± 0.9
Investigate	0.18	0.10	− 0.60	0.18	0.09	− 0.07	8.5 ± 1.1	12.9 ± 1.0
Sniff towards	0.24	0.25	0.22	0.25	− 0.18	− 0.78	1.7 ± 0.5	3.3 ± 0.7
Defend	0.21	− 0.54	− 0.05	− 0.03	0.10	− 0.10	3.9 ± 0.6	5.3 ± 0.7
Shove	0.06	− 0.54	− 0.27	− 0.30	0.01	− 0.09	1.1 ± 0.2	2.4 ± 0.5
Attack	0.37	− 0.15	0.35	0.00	0.30	0.09	3.4 ± 0.6	4.4 ± 1.1
Chase	0.33	0.17	0.27	− 0.11	0.48	0.23	1.3 ± 0.3	1.8 ± 0.9
Fight	0.01	− 0.25	0.23	0.75	− 0.16	0.35	0.7 ± 0.3	0.3 ± 0.2
Squeak	0.33	− 0.38	0.12	0.06	− 0.07	− 0.25	2.4 ± 0.5	4.9 ± 0.9
Sit by	− 0.30	− 0.15	− 0.24	0.41	0.18	− 0.08	2.5 ± 0.6	0.9 ± 0.3
Allogroom	− 0.30	− 0.08	0.01	0.15	0.75	− 0.31	0.4 ± 0.2	0.1 ± 0.1

*Mean ± SE of interactions in which behaviour was shown. See text for comparison of the number of interactions per trial.

component only, which represented a clear comparison between the initiation of interactions and aggression versus static defensive behaviour (defend, squeak and shove) and explained 30.8% of the variance in individual behaviour. Within each dyad there was a much greater difference in scores when the mice met in a neutral area than when one mouse was a prior resident ($F_{1,41}=13.6$, $P<0.001$), suggesting that there was much greater differentiation between an aggressor and defender within a neutral area. The greater proportion of interactions involving aggression found in resident enclosures was thus due to both members of a dyad, in opposition to the prediction of the aggressive exclusion hypothesis but in agreement with the dominance hypothesis if mice readily compete for dominance over occupied areas.

DISCUSSION

Results from all of the tests carried out provide evidence against the hypothesis that *M. spretus* fiercely attempt to exclude others from their territory, but support the hypothesis that the mice establish dominance relationships using stylized postures of submission and are relatively tolerant of each other's presence once these relationships are established. The mice also appeared to use odour cues to identify, and then compete for dominance over, occupied areas.

Competitive Behaviour

Perhaps the strongest evidence against aggressive exclusion was the nature and extent of the aggression. The relatively infrequent occurrence of chasing, which was always brief and tended to be seen in the first few encounters only, the use of stationary defensive postures by subordinates (whether attacked or not) rather than attempted flight from the area, and the frequent approaches by defensive mice towards their opponent even after they had been attacked, do not suggest that these mice are highly intolerant of unfamiliar conspecifics and aggressively exclude each other from individual territories. While it is possible that the artificial nature of our test environments may have altered their natural responses to some extent, the highly stylized nature of the subordinate's submissive posturing and 'shove' behaviour, with the common result that the aggressor (or potential aggressor) usually moved away and often only briefly investigated the subordinate subsequently, indicates that this was a natural and functional pattern of behaviour. Hurst et al. (1994) described similar defensive posturing in both intra- and inter-sexual dyadic encounters in this species. In this earlier study, mice were separated immediately they started chasing as it was expected that aggression would escalate rapidly if the mice were attempting to chase others out of their normally large territories (Cassaing & Croset

1985), and such aggression was taken to indicate social intolerance. However, our current study has shown this not to be the case. In established populations of *M. domesticus*, in contrast, intruders and subordinates usually take flight on encountering a dominant male within his territory (Hurst 1993) and chasing of unfamiliar intruders by territorial males and females can be extensive, even by subdominant residents (e.g. see Rowe & Redfern 1969). This is the behaviour expected of mice attempting to exclude others from their territory.

It might be argued that resident mice in our study were not established for long enough to induce strong territorial behaviour, or for intruders to recognize them as highly aggressive territory owners and flee. Residents were established only a day prior to tests as we wanted to examine normal social responses shown by experienced mice caught from the wild, and prolonged isolation greatly reduces social tolerance in *M. domesticus* (e.g. Goldsmith et al. 1976). However, since the enclosures used were very small compared with their normal home range, enclosures were likely to become highly familiar and suffused with a resident's odour after only a few hours. Our results showed that this prior residence was sufficient to induce territorial defence (residents showed aggression more readily than their intruder opponent) even though this did not guarantee dominance; intruders also responded strongly to resident odours but in a direction predicted by the hypothesis of territorial dominance not by that of aggressive exclusion. The duration of residence thus does not appear to have been a major limiting factor.

Both prior residency and body size were important factors in determining interactions. While prior residency increased the likelihood that the mice would initiate aggression against a conspecific, the relative weight difference between the mice appeared to be the most important factor determining their interactive behaviour, especially in open enclosures. Competitive ability thus appears to depend largely on relative size in this species. It was notable that when mice were of similar size, one often stood up in defensive posture and shoved the other with its forepaws. This behaviour seems to represent an ambiguous response, where mice were unwilling to challenge with aggression but were not willing to let their opponent too close. Shoving might even be a

mechanism for judging the strength and thus relative competitive ability of their opponent, or to show their own strength and inhibit an aggressive challenge.

This is not to say that *M. spretus* always tolerate the presence of other conspecifics, particularly in encounters between two highly competitive individuals, and we found much variability in aggressiveness between mice. Aggression was greatest from lactating females or when two adult males initially fought for dominance, although even then chases were only brief. In other years, we terminated a small number of trials involving *M. spretus* from the same study sites early to prevent a few highly aggressive and intolerant individuals from hurting their opponents during persistent attacks and chases, but such intolerance was rare (found in only four of 313 dyad pairings during 1992–1994: J. Hurst, unpublished data). As our trap records indicated that we caught and tested virtually all the adult mice using our study sites, it is very unlikely that this very small proportion of dyads could maintain the wide dispersion of the mice through aggressive intolerance. Cassaing (1984) found much stronger aggression in encounters between male *M. spretus* after isolating subjects in heterosexual pairs for at least 3 weeks prior to testing, but similar low aggression when individuals were tested at capture. Their tolerance may thus be conditioned by experience of recent contact with conspecifics and the difficulty of defending natural sites.

One striking feature of *M. spretus* behaviour was that subordinates of both sexes repeatedly approached and sat next to their aggressor, immediately rearing into a defensive posture when the aggressor paid any attention to them. This was particularly obvious when defensive subordinates went to sit by aggressors that were feeding in the food pot, but did not feed themselves. The result of this contact was that the subordinate was investigated occasionally but not attacked again whereas those that separated were likely to suffer another attack if they were re-encountered later. If mice have to establish dominance relationships each time they meet an opponent (odour cues are not likely to provide a reliable signal of status if cheats can easily evade challenges and hide in the area), it may be to the benefit of a weaker competitor to maintain continuous contact and reduce the chance of being attacked again while a dominant individual is in the area. Persistence in the

area and the use of clear submissive postures rather than ready flight by intruders will make it more costly for the dominant to exclude them, so the latter is less likely to attempt to chase them from the area. Their approaches may thus function to maintain familiarity and recognition of their established relationship with the aggressor.

Use of Odour Cues

One of the most interesting findings was that the presence of odour cues appeared to increase challenges for dominance, resulting in relatively more intruder attacks against a matching resident than against a non-resident, and more mutual fighting within occupied than within unoccupied areas. This suggests that the mice may be more inclined to compete for dominance in areas that appear suitable to support the species. At first sight, this seems at odds with a previous finding that *M. spretus* were much more likely to show defensive than ambivalent behaviour after entering a tunnel bearing the odour of their opponent (Hurst et al. 1994). In this earlier study, however, the difference in defensive behaviour concerned whether the mice had had prior exposure to a conspecific's odour, which always happened to be that of their opponent. For comparison, intruders in the present study, all of which had prior exposure to conspecific odour, also showed significantly more defensive behaviour than their opponents (residents in clean tunnels) which had not had prior odour experience (frequency of nose up and eyes closed, matched-pair $t=3.31$, $df=26$, $P<0.01$), regardless of whether the opponent matched the odour previously encountered by the intruder. Given the willingness of mice to compete in areas soiled by mouse odour, it is not surprising that they readily show defensive postures that assuage attack when in these areas. Our results suggest that *M. spretus* use conspecific substrate odours to recognize when they are entering a potentially occupied area where they might be attacked, and use such cues to identify but not to avoid challenging a resident in the area, a response that would have been expected if residents scent mark their territory to advertise their dominance and potential danger to unfamiliar intruders (Gosling 1982; Gosling & McKay 1990).

Further evidence to support the hypothesis of avoidance of dominant competitors comes from the very strong attraction that mice of both sexes showed towards nest sites bearing the fresh odours of unfamiliar conspecifics. Although a previous study (Hurst et al. 1994) found that mice were initially attracted to investigate the entrances of similar soiled tunnels, any bias towards tunnels was lost in the present study when mice were given the opportunity to enter and explore them. This indiscriminate investigation of tunnels but strong bias towards nests is likely to reflect the need of the mice to move through and explore many different areas in search of food or to find their way home, while only a few sites will offer suitable protection for resting and nesting. Using conspecific odour cues to select resting sites may help in the difficult task of finding reliable sites that will provide good protection from predators, and from inclement weather if conditions changed for the worse. Although the ground in our two study areas was covered extensively by grass and shrubs, the mice were restricted to certain areas where the cover was dense or where they were protected by thick brambles, gorse or a heap of cut or fallen tree branches, and where the ground did not become very damp or flooded in heavy rain. Thus, the choice between a clean versus a conspecific's nest may not have represented a simple choice to the mice between 'unoccupied and available' versus 'occupied and unavailable' but otherwise equivalent sites. Instead, a clean nest within an otherwise occupied area is likely to indicate a site judged unsuitable by another conspecific already using the area, while the resident nest represents an apparently suitable and preferred nest site but with competition for access. It is interesting to speculate that the distribution of faeces near the tunnels and away from the nest may have been an attempt to avoid leaving cues near resting sites that advertised their occupation (to conspecifics or predators), although it could be simply a hygienic attempt to keep excreta away from resting sites (Hurst & Smith 1995).

Could the need to find a suitable habitable site in our artificial test situation be overriding a normal tendency to avoid the territories of other mice that intruders would show if within their own home area? Our results suggest this not to be the case since they still preferred to visit and enter a conspecific's nest even when their own was available. This does not eliminate the possibility that mice might choose to avoid the odour of a familiar resident after experiencing aggression from this particular individual (e.g. Jones &

Nowell 1989). *Mus spretus* appear to avoid entering tunnels of near neighbours but not those of unfamiliar conspecifics (Hurst et al. 1994). Thus, having established dominance by direct interaction, spatial dispersion might result from the subsequent avoidance of known dominant competitors that have priority of access to the most suitable sites within an area. By using such learnt association, substrate odours could provide a reliable signal of relative competitive ability even over large complex areas. However, the relationship between dominance establishment and subsequent response to an opponent's odour remains to be tested in this species.

Our results thus suggest that there is a major difference in social behaviour and the use of odour cues between *M. spretus* living in grassland on scattered resources and the widespread commensal *M. domesticus* which defends small territories when resources are concentrated by human activities. However, it is possible that the novel methods of testing and analysis used in our study, using recently captured animals, would fail to elicit the behaviour patterns predicted by the aggressive exclusion hypothesis even in commensal *M. domesticus*. To establish that these differences are genuine, a subsequent study has repeated these tests using *M. domesticus* freshly captured from farm buildings to allow direct comparison (unpublished data).

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