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Excluding neighbours from territories: effects of habitat structure and resource distribution

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Small animals vulnerable to predation, such as rodents, have a strong preference for sites that provide physical protection from predators. This is likely to affect not only their use of space and activity but also the ease with which they can defend a territory, since the likelihood of encountering (or losing) intruders and their willingness to compete are affected by the quality and distribution of resources and the structural complexity of the habitat. To examine how these different habitat factors interact to influence territorial behaviour in male house mice, *Mus domesticus*, which inhabit environments with very different levels of complexity and resource distribution, we housed male–female pairs in enclosures representing one of eight habitat types varying in ground-level structure (open/complex), overhead cover (present/absent) and distribution of protected nest sites and food (resources clumped together/scattered). Neighbouring pairs were allowed to interact five times over 3 days and we examined behaviour during the first (unfamiliar) and fifth (familiar) periods. Initially, encounter rates were two to three times higher in open habitats with overhead cover than in either complex habitats or open habitats without cover, and higher when resources were scattered than when they were clumped. Aggressive interactions between unfamiliar males were more prolonged in habitats with open ground-level structure, where pursuits followed restricted pathways. The effects of overhead cover on aggression among unfamiliar neighbours unexpectedly depended on the origin of the mice. Once neighbours learnt the outcome of their interactions, aggressive interactions were most prolonged in habitats with scattered resources and complex ground-level structure, making these habitats the most difficult to defend.

It is well established that the quality and distribution of resources (e.g. food, nest sites) can affect how easily and effectively territories can be defended. Resources can be monopolized easily if concentrated in a small number of sites, but are harder to defend when scattered (Magnuson 1962; Monaghan & Metcalfe 1985; Grant & Guha 1993). Thus, habitats containing scattered resources may support a greater number of social groups and a higher density of animals than habitats containing equivalent resources that are clumped (e.g. Stueck & Barrett 1978; Noyes et al. 1982). The distribution and quality of resources also influence the attractiveness of different parts of a territory to both residents and intruders, with animals willing to invest more in acquiring or defending valuable resource sites (e.g. Johnsson et al. 2000; Gray et al. 2002).

For animals that are small and vulnerable to predation such as rodents, the structural complexity of the local habitat and the distribution of protected nest sites can be extremely important in providing appropriate cover and protection from predators. Thus, rodents typically have a strong preference for sites with a high degree of structural complexity, and their movement patterns and choice of nest sites are strongly influenced by the microhabitat (e.g. Hansson 1982; Adler 1985; Manson & Stiles 1998; Jensen et al. 2003). However, the structural complexity of a habitat can increase the difficulty of defence if intruders or subordinates can hide easily from resident aggressors (e.g. Poole & Morgan 1976; Gray et al. 2000). On the other hand, animals might be reluctant to compete in open habitats if there is inadequate cover from

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predators. Physical habitat structure is thus an important factor in determining the quality and attractiveness of a territory to vulnerable small mammals, as well as influencing how easily the territory can be defended from competitors. However, as yet, we have little understanding of how different aspects of habitat structure and resource distribution interact in determining territory quality and ease of defence, or their relative importance.

We examined how the distribution of protected nest sites, presence of overhead cover and complexity of ground-level structure influence rates of encounter and competitive interactions between neighbouring male house mice, *Mus domesticus*, living in mixed-sex pairs. House mice prefer to live commensally in the human-built environment, where they can exploit animal feeds and human food stores and are protected from harsh weather conditions (Berry 1981). Social structure and spatial overlap appear to vary widely between habitats (reviewed by Bronson 1979; Berry 1981; Barnard et al. 1991). Such habitats vary considerably in their level of physical complexity and resource distribution, but specific features can be modelled relatively easily under controlled laboratory conditions to examine the influence and interactions between each factor. Sheds and garages, for example, are open areas when empty but physically very complex when full of stored objects. Grain stores are usually open with no internal structuring but with widespread food, storerooms have a more complex arrangement with objects and resources distributed unevenly, while livestock-holding pens are often open areas with clumped or scattered food resources and subdivided into sections by internal walls. Humans, cats and dogs maintain a strong 'predation' pressure on mice to remain hidden from view and to have ready access to safe nest sites and refuges that provide physical protection. In open habitats that have little ground-level structure and no overhead cover, mice spend much of their time within protected refuges and make only limited use of the habitat when active, staying close to walls and other objects even in total darkness (Gray et al. 2000; Jensen et al. 2003). However, mice are much more active if the habitat contains extensive ground-level structuring, and can make greater use of the habitat while still remaining close to vertical surfaces and other objects throughout their home area. Overhead cover has little additional effect on use of space and activity in the presence of ground-level structure, but is attractive in otherwise open habitats and is used when fleeing from a potential predator (Jensen et al. 2003). We might therefore expect that, when animals are at risk of predation, territories will be most difficult to defend in habitats with complex physical structuring (particularly at ground level) and scattered resources. If structure within the habitat reduces predation risk and is thus perceived as desirable, both intruders and residents may be willing to escalate aggression, as seen in some territorial fish (Martel & Dill 1993), leading to more extended aggressive encounters that are both risky and energetically costly to both parties.

Conversely, we expect territories to be easiest to defend in open habitats with clumped resources that can be monopolized easily because (1) mice will stay close to what little ground-level structure is available in open habitats, providing residents with a much smaller area to patrol and defend; (2) intruders will have fewer places to hide and will be less willing to compete; and (3) the absence of structure will increase the perceived predation risk so that opponents displaced from protected sites will flee from the area (Hurst et al. 1996).

Following on from our study of the activity and use of space among house mice in the absence of intruder pressure (Jensen et al. 2003), we thus examined how the complexity of ground-level structure, presence of overhead cover and distribution of protected nest sites interact in determining rates of encounter, competitive behaviour, resolution of conflicts and territory invasion among neighbouring males. Since the intensity and outcome of interactions with competitors is likely to depend on experience of previous interactions (see review by Stamps 1994), we examined behaviour between neighbouring competitors both when they first met and once they had had the opportunity to interact several times and learn the outcome of their interactions.

METHODS

Habitat Types

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