Mechanisms of competition among insectivorous mammals

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Summary. This study investigates the mechanisms of competition between congeneric pairs of insectivorous mammals in two communities in Australia and England. Direct field observations showed that physical interactions between species do not occur, whereas conspecific encounters are frequent. In field enclosures the smaller, subordinate species in each community (Antechinus stuartii: Marsupialia: Sorex minutus: Eutheria) remained alert in the presence of the dominant species (A. swainsonii, S. araneus), and moved quickly away when the latter approached. The rate of prey capture by subordinate individuals also increased immediately after removal of the dominants. Hourly removals of some individuals of the dominant species in each community over 24 h produced hourly increases in the numbers of subordinate individuals that were captured. The rapidity of these responses suggests strongly that the dominant insectivores in each community interfered with the resource use of the subordinate species. Biomass of invertebrates increased inconsistently or slowly within 3 months of removal of the dominant insectivores; hence the rapid responses by subordinate individuals in experiments were not due to simple exploitation or tracking of resource levels. The subordinate insectivores probably detected and avoided contact with dominants instantaneously using auditory or olfactory cues; reciprocal avoidance of congeneric odours was demonstrated using odour-scented traps. Insectivorous mammals may usually compete by interference (or encounter competition, sensu Schoener 1983). For dominant species within communities the cost of interference is minimal and the benefit of gaining exclusive access to resource-rich microhabitats is high. Conversely for subordinate species the benefit of temporarily exploiting the same rich microhabitats may exceed the small costs of vigilance and movement to nearby refugia.

Key words: Competition – Antechinus – Sorex – Interference – Insectivores

Although interspecific competition probably occurs in many ecological systems and may have important effects on species distribution and abundance (Schoener 1983), we have relatively little understanding of the mechanisms by which competition occurs. Yet, knowledge of the mechanisms of competition is crucial, both for predicting individual behaviour and resource use and for understanding community processes (Tilman 1987).

Traditionally, two mechanisms of competition have been distinguished. “Interference” refers to situations where individuals directly reduce each others’ access to shared resources, as by fighting, whereas “exploitation” refers to situations where individuals affect each other indirectly by utilizing resources and depriving others of their benefits (Park 1954; Miller 1967). Case and Gilpin (1974) argued that interference is the most widespread form of competition in nature, while Miller (1969) concluded further that interference is the “more highly evolved” of the two mechanisms. More recently, Schoener (1983) noted that the terms “interference” and “exploitation” are often confused in the ecological literature, and proposed a new terminology that distinguishes six mechanisms of competition.

Among mammals, interference competition (including encounter and territorial competition sensu Schoener 1983) has been inferred from observations of interspecific territoriality and fighting (Brown 1971; Frye 1983; Wolff et al. 1983), from microhabitat segregation at high but not at a low population density (Dickman and Woodside 1983; Abramsky and Pinshow 1989) or from rapid responses by species in experiments where putative competitor species have been removed (Lemen and Freeman 1983, 1986; Fox and Pople 1984). Further inferences about interference have been drawn from observations that some species avoid congeneric or confamilial odours (Daly et al. 1980; Stoddart 1980; Randall 1981); however, the effectiveness of this form of interference is not known.

In contrast, exploitation or consumptive competition (Schoener 1983) has been inferred mostly from observations of differential food or microhabitat use among
coexisting species (Gliwicz 1981; Montgomery 1981; Schroder 1987). Relatively slow responses of species to competitor removal may also suggest some form of exploitation because there is presumed to be a time lag between depletion and recovery of resource levels (Munger and Brown 1981). However, this suggestion has not been critically tested, and it is unclear how slow a response must be before exploitation, rather than interference, can be implicated.

In this study, I attempt to distinguish the importance of exploitative and interference mechanisms of competition in two simple communities of insectivorous mammals. In each community competition is asymmetrical, with the larger of two species restricting the numbers and microhabitat use of the smaller; competition probably occurs for food (Dickman 1986a, b, 1988a, 1989).

Five major questions are addressed:

1. Do direct (encounter or territorial) interactions occur between the species?
2. Do indirect (olfactory) interactions occur between the species?
3. Does the dominant species affect the rate of capture of prey of the subordinate species?
4. How quickly do the subordinate species respond to changes in the numbers of the dominant?
5. How quickly do resource (prey) levels respond to changes in the numbers of the dominant species?

These questions are addressed by observing animals under natural and enclosed conditions in the field, by observing the responses of animals to traps scented with conspecific and interspecific odours, and by assessing the responses of the subordinate species and prey populations to fluctuations in the numbers of the dominant species.

Materials and methods

Animal communities and study areas

The first community comprised two species of dasyurid marsupials, Antechinus swainsonii (ca. 50 g) and A. stuartii (ca. 20 g). Both species occur in forest and heath over much of south-eastern Australia, with A. stuartii extending slightly further inland into woodland (Dickman 1982). Both species take a variety of invertebrates, although A. swainsonii also feeds occasionally on small skinks and berries (Green 1972; Hall 1980; Dickman 1986a).

Observations on Antechinus were made in seven study areas (1.72 - 3.70 ha) in the Bemudabella Range, near Canberra, Australian Capital Territory, between May 1978 and March 1982. The habitat in each study area is a tall dense forest of Eucalyptus viminalis, E. radiata and E. fastigata, with understory shrubs Acacia dealbata, A. melanoxylon, Pomaderris aspera and Rubus fruticosus, and a dense understory of ferns Blechnum nudum and Pteridium esculentum (Florence 1973). All study areas are situated in valley floors along the banks of creeks at altitudes of 740–825 m.

The second community comprised two species of eutherian shrews, Sorex araneus (ca. 7 g) and S. minutus (ca. 4 g). These species are widespread throughout much of Europe in grassland, scrub and woodland habitats. Both species eat a wide range of invertebrates (Perretta 1976; Churchfield 1982).

Observations on shrews were made in eight study areas (0.4–2.0 ha) within the City of Oxford, England, between November 1982 and July 1984. Each study area is rough grassland dominated by Dactyliosperma sp., Pileum pratense, Agropyron spp. and Arrhenatherum elatius, with patches of herbs Urtica dioica, Ranunculus spp., Cirsiurn spp., Vicia spp. and isolated clumps of blackberry Rubus fruticosus. The study areas are enclosed by roads, buildings or watercourses, which appear to severely limit the movements of shrews (Dickman and Doncaster 1987).

Trapping

Live-traps were used to carry out short- and long-term manipulations of animal numbers in each study area, and to investigate olfactory interactions. In Australia, Elliott aluminium live-traps were set on grids or lines at intervals of 5–15 m. Most traps were set on the ground, but, to capture A. stuartii, small numbers were also placed in the lower limbs of trees. Traps were baited with rolled oats, peanut butter, honey and bacon, provided with grass or cotton wool for bedding, and checked in the morning and sometimes evening for 3–12 days a month. In England, shrews were trapped in Longworth traps baited with meat or fly pupae, after a pre-baiting period of 24–36 h. Traps were set 10 m apart on grids, and checked twice daily for three consecutive days a month. All captured mammals were identified, weighed, sexed, toe-clipped and released at the point of capture. Population estimates in each study area were expressed as the minimum numbers of animals known to be alive each month (Krebs 1966).

I investigated the speed of response of the subordinate species in each community to changes in the numbers of the dominant species by effecting short-term reductions in the numbers of the dominant in portions of study areas where animal numbers were relatively high. Traps were checked hourly for 24 h, and some individuals of the dominant species were removed for 1–3 h. In all experiments removals reduced the local numbers of the dominant species, on an hourly basis, to 0–90% of the numbers known to be alive. The responses of the subordinate species in each community were assessed simply by counting the numbers of subordinate individuals captured per hour throughout the 24-h experimental periods. The results of long-term removal experiments have been presented elsewhere, and are not further discussed (Dickman 1986a, b, 1988a and unpublished).

To detect indirect olfactory interactions between species, I used odour-impregnated traps. In each study area, in some months, I set three aluminium traps at randomly selected trap stations. One was “baited” with cotton wool containing the faces, urine and other bodily odours of one of the competing species in the community, the second was baited similarly with cotton wool containing the odours of the second species, the third contained odourless cotton wool. Odour-impregnated cotton wool was obtained either from captive animals or from individuals captured in traps off the grids, and was used within 6–24 h of collection. All traps were cleaned prior to use in deodorizing detergent and handled with gloves in the field. The traps were set in "Y"-shaped clusters, with their entrances facing inward, 10–15 cm apart, to ensure equal probability of encounter for visiting mammals. Used traps were replaced immediately; the impregnated cotton wool in unused traps was replenished every 24 h. The responses of small mammals to interspecific odours are assessed by counting their frequencies of capture in each trap, and testing for association by \( \chi^2 \). Differences in the level of association between species are detected by comparing the deviation of expected and observed values in each cell of the contingency tables, and expressing this as a percentage of the expected values (Simpson et al. 1960).

Field observations

Animals were observed directly under natural conditions in the field to assess whether encounter or territorial interactions occur. Antechinus species were observed in two study areas near nest sites.