

Experimental confirmation of interspecific competition between native and introduced mice

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Abstract

This paper tests the hypothesis that *Pseudomys novaehollandiae* shows competitive superiority over *Mus musculus*. Experimental removals of *P. novaehollandiae* on four 1 ha treatment plots and additions on a further four 1 ha plots show significant effects of interspecific competition when compared to two 1 ha unmanipulated control plots. Significant effects of *P. novaehollandiae* populations on the abundance of *M. musculus* populations were observed for number of captures/day, abundance/trapping session and for the recruitment of new individuals over the post-removal period, thus allowing rejection of the null hypothesis in each case. There was an apparent ceiling on the total rodent abundance which is indicative of a resource limitation. The resource in short supply appears to be space, but it is not clear if the competition is for food or shelter resources contained within such space or for the space per se, but the latter seems less likely.

The confirmation of this interspecific competition supports the inferences drawn from a considerable amount of indirect evidence, largely descriptive, obtained from previous studies in the Myall Lakes National Park. This study also shows that competition is one of the mechanisms controlling the replacement of species in the succession following disturbance and lends support to the habitat accommodation model proposed for such succession. These points support previous statements on the importance of interspecific competition as a determinant of the structure of these small-mammal communities.

Introduction

This paper describes the results of a manipulation

experiment designed to test the hypothesis that the New Holland mouse (*Pseudomys novaehollandiae*) competes with, and inhibits population size of the house mouse (*Mus musculus*). *Pseudomys novaehollandiae* was removed from four treatment plots and the response of *M. musculus* on these plots compared with that on two unmanipulated control plots. The bases on which this hypothesis was established are now developed.

The results of a number of extensive and intensive studies in the Myall Lakes National Park have implied a competitive interaction between *P. novaehollandiae* and *M. musculus* (Fox 1980). The indirect evidence supporting this hypothesis follows (from Fox 1980):

(1) The species show reciprocal abundance; where *P. novaehollandiae* numbers are high, *M. musculus* numbers are low and vice versa.

(2) They show reciprocal population trends at the same site; when *P. novaehollandiae* numbers increase, *M. musculus* numbers decrease and vice versa.

(3) A habitat shift is shown by *M. musculus* as *P. novaehollandiae* numbers increase. No equivalent habitat shift occurs for *P. novaehollandiae* when *M. musculus* numbers increase.

(4) *Mus musculus* spatial niche breadth is significantly negatively correlated with *P. novaehollandiae* abundance; the converse shows no significant correlation.

(5) High dietary overlap and high between-habitat spatial overlap exists; however, within-habitat spatial overlap is low.

The results of a study of the recolonization of sand-mined forest carried out in 1982 add further weight to the development of our hypothesis (Fox & Fox 1984). Not only do these species show reciprocal abundance but there is a marked species replacement as *P. novaehollandiae* appears to displace *M. musculus*, as part of the small-mammal succession, illustrating the prediction made from regenerating sand-mined heathland (Fox & Fox 1978).

Taking all of this indirect evidence into account, the development of our hypothesis on the nature of the interaction between these species is clear. Our experiment was designed to test the null hypothesis of no interspecific competition between *P. novaehollandiae* and *M. musculus* with the alternative hypothesis that *P. novaehollandiae* interacts competitively with, and shows superiority over, *M. musculus*. As direct evidence for competition can only be provided by manipulation of field populations we tested this hypothesis by monitoring the effect of *P. novaehollandiae* removal on *M. musculus* abundance on treatment plots compared to that on unmanipulated control plots.

Pseudomys novaehollandiae has a coastal distribution in New South Wales, Victoria, Queensland and Tasmania, but was not rediscovered (Mahoney & Marlow 1968; Keith & Calaby 1968) until 80 years after its first capture. The question of its distribution and abundance being restricted by *M. musculus*, as has been claimed for other native rodents, has often been raised (Newsome *et al.* 1975; Newsome & Corbett 1975). Posamentier and Recher (1974) found *P. novaehollandiae* to be patchily distributed on the east coast of New South Wales, but not uncommon where it did occur. The distribution and abundance of *M. musculus* from the same survey indicated that it only occurred where *P. novaehollandiae* was absent or rare. Posamentier and Recher suggested that *M. musculus* partitioned available resources with *P. novaehollandiae*, occupying a niche left vacant by the absence of this native species. This interpretation was further supported by a more detailed study (Posamentier 1976). Both species were found to be most abundant on areas recently burned, as had already been suggested for *P. novaehollandiae* (Keith & Calaby 1968).

Although its distribution covers the entire continent, the house mouse has been present in Australia for less than 200 years. It has been referred to as *M. musculus domesticus*, and then *M. domesticus* (Marshall & Sage 1981, p. 1923). We will continue to refer to it as *M. musculus* [following the terminology used in Strahan (1983)]. A number of studies have dealt specifically with the population ecology of this species in Australia (Newsome 1969a, b; Newsome & Corbett 1975; Saunders & Giles 1977; Thomson 1980).

The position of *M. musculus* in the Australian fauna as an opportunist or fugitive species, abundant in early seral stages, was supported by Recher *et al.* (1975) and Newsome *et al.* (1975). Newsome and

Corbett (1975) went further and advanced the thesis that in the arid central regions of Australia *M. musculus* exploits the environment more effectively than the native species resulting in declines in their abundance and distribution. While Newsome and Corbett (1975) were not dealing specifically with the coastally distributed *P. novaehollandiae* their implication that similar mechanisms operate to the detriment of the small native species was clear. This was borne out with the suggestion of the competitive exclusion of *P. novaehollandiae* by *M. musculus* at Nadgee (Newsome *et al.* 1975).

The effect that these two species have on one another has remained an important factor in the interpretation of the results of studies of *P. novaehollandiae* and the early seral stages of disturbance by fire or mining (Kemper 1977; Fox & Fox 1978, 1984; Fox 1980, 1982a; Thomson 1980; Fox & McKay 1981; Kentish & Bourne 1982).

Braithwaite *et al.* (1978) recognized five food niches for small mammals in south-eastern Australian lowland heath. Based on the diet analysis of Watts and Braithwaite (1978), *P. novaehollandiae* was allocated to the generalist herbivore niche while *M. musculus* was seen to occupy the niche of insectivore (either soil fossicking or scansorial). They also saw *M. musculus* as occupying a niche not being utilized by native species, rather than displacing native species as suggested by Newsome and Corbett (1975). Braithwaite *et al.* (1978) comment on the absence of a granivorous niche in these heathlands and hence the absence of mammal species in this niche. However, Thomson (1980) found that both *P. novaehollandiae* and *M. musculus* consumed a large seed component in their diet and as a result Fox (1980) incorporated a sixth food niche (generalist granivore) in the description of the small-mammal community at Myall Lakes (NSW). Cockburn (1980) confirmed the role of *P. novaehollandiae* filling a granivore niche at Reeves Beach (Victoria) where it has previously been regarded as a generalist herbivore (Braithwaite *et al.* 1978). In this case *M. musculus* fills a more omnivorous niche.

Methods

Two control plots were established on an area regenerating after sand mining, where topsoil had been replaced between December 1975 and February 1976. These plots occupied almost the full

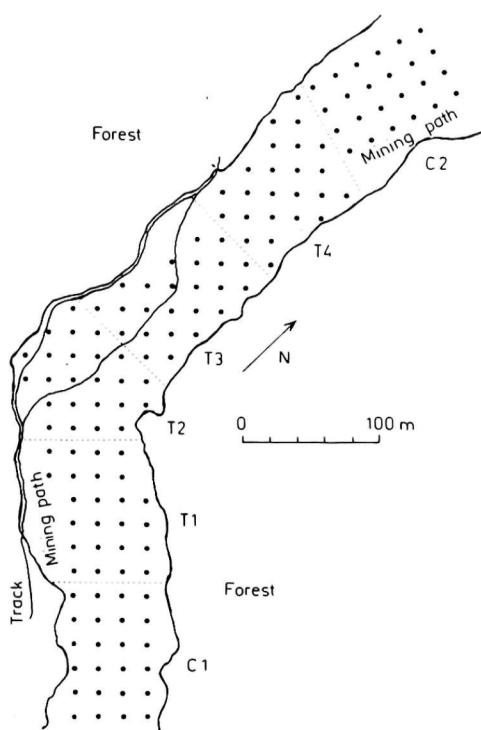


FIG. 1. Map of the trapping grid established along the regenerating mining path. The two control plots at either end, are indicated as C1 and C2 while T1-T4 label the four treatment plots.

width of the mining path with four rows of six traps using a 20 m trap spacing. The mining path was regenerating as heathland and formed a strip of heath amidst the undisturbed open-forest. Four treatment plots (each with 24 trap stations), were established between these two control plots so that they were contiguous with each other and with the control plots (Fig. 1). Regeneration on these areas is described by Fox and Fox (1984) where the two control plots are identified as BG3 and BG4.

One $9 \times 10 \times 33$ cm Elliott collapsible aluminium small-mammal trap was set at each trapping station. Traps were baited with peanut butter and oatmeal and checked early the following morning. All animals were individually marked by toe clipping and at each capture they were identified to sex, species and individual while trap station and reproductive condition were recorded. Pre-manipulation density estimates were available from work in April 1982 (Fox and Fox 1984) and from trapping for the four nights from 13 to 16 October 1982.

The removal of all *P. novaehollandiae* caught on the treatment plots and their relocation more than 1.3 km further along the mining path began after

traps were checked on 16 October, the only exceptions were animals caught on the treatment plots but previously caught on one of the two control plots and considered resident there. *Pseudomys novaehollandiae* were continually removed from the 17 to 19 October when this pulse removal was terminated. Further trapping sessions were carried out on 24–25 October, 5–8 November and from 30 November to 2 December to monitor the effect of this perturbation, but no further *P. novaehollandiae* were removed. Return to equilibrium was assessed by a final trapping session from 2–5 April 1983.

The animals removed were relocated to an area abutting an already established plot [BG1 in Fox and Fox (1984)]. This plot was to act as an unmanipulated control while the *P. novaehollandiae* were released onto three treatment plots adjacent to it (T5, T6, T7). The control plot (BG1) had been trapped in April 1982 (Fox & Fox 1984) and was also trapped from 13–16 October, 17–19 October, 24–25 October and 5–8 November, concurrently with the removal experiment. The treatment plots (T5, T6, and T7) were trapped for the latter four periods with animals being introduced from 16 October 1982 to 19 October.

The Mann–Whitney U-test (Siegel 1956, p. 116) was used for comparisons between control and treatment plots for the number of captures each day, number of animals per 100 trapnights (TN) for each session and the number of new animals per 100 TN for each session as these were not normally distributed. With the *a priori* expectation that *M. musculus* treatment values will exceed control values and the reverse for *P. novaehollandiae* one-tailed tests on significance were used.

Results

During the removal period 17–19 October, a total of 26 *P. novaehollandiae* were removed from the four treatment plots (19 females and 7 males). Two males returned 1.5 km along the mining path from the relocation site and had to be removed again. No other relocated animals were captured on either the control or experimental plots.

Captures per day

The number of captures each day on control and treatment plots are shown separately for *M. musculus* (Fig. 2a) and *P. novaehollandiae* (Fig. 2b). To simplify presentation the mean value per plot is

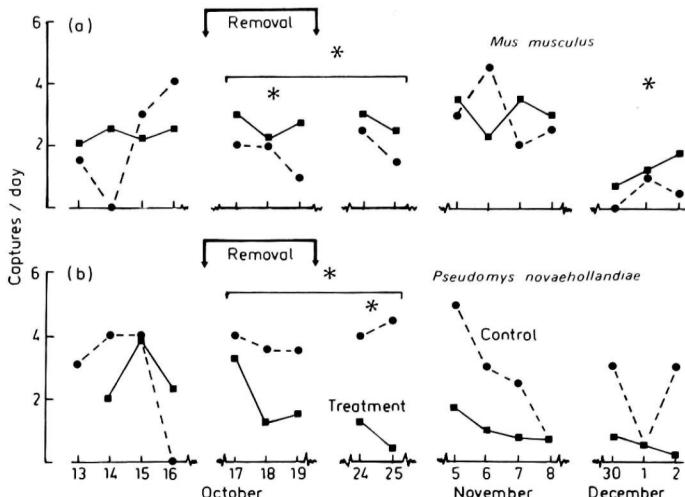


FIG. 2. The mean number of captures per plot for each trapping day. The control plot means are shown with round symbols and dashed line while treatment plot means are shown as square symbols with a solid line. The removal period (17–19 October) is marked on the figure and stars are used to show significant differences between treatment and control plots (Mann–Whitney U test, $P < 0.05$) for single or pooled trapping sessions. (a) *Mus musculus*. (b) *Pseudomys novaehollandiae*.

graphed, but values for each individual plot were used in statistical tests. For the period before removal (13–16 October) there is no significant difference between control and treatment plots for either species. During the removal period (17–19 October) the number of *P. novaehollandiae* caught decreased but overall there was no significant difference between control and treatment plots (Fig. 2b). However, for the next trapping period (24–25 October) there were significantly fewer *P. novaehollandiae* caught each day on treatment plots than on control plots ($P=0.014$, $n_1=4$, $n_2=8$, Mann–Whitney U-test). This significant difference was maintained when tested over the post-removal period 17–25 October ($0.001 < P < 0.01$) but lost significance for the next two trapping periods.

During the removal period (17–19 October) significantly more *M. musculus* were captured each day on the treatment plots than on the control plots ($0.025 < P < 0.05$) but the difference was not quite significant for the two day trapping period, 24–25 October ($P = 0.077$) (Fig. 2b). However, there was a significant difference for the post-removal period from 17 to 25 October ($0.001 < P < 0.01$). There was no significant difference in the November trapping period but in the last trapping period (Fig. 2b) more *M. musculus* were captured on the treatment plots than on controls ($0.001 < P < 0.01$).

Abundance per session

A similar result can be seen if one analyses the

number of individuals caught per 100 trap nights at each session (Fig. 3). In this way individuals recaptured within a trapping session do not further contribute, so the measure represents the abundance for each species. For the period 17–25 October there are significantly more *M. musculus* present on treatment plots than on controls ($P = 0.0418$, see Fig. 3a) in response to the significant decrease in *P. novaehollandiae* abundance for the same period ($P = 0.024$, see Fig. 3b). The trapping sessions are shown with correct scaling on the time axis, except for the April trapping periods. The abundance of *P. novaehollandiae* in April 1983 is very close to that in April 1982 and indicate that *P. novaehollandiae* had recovered to its pre-manipulation abundance.

Total rodent abundance

The effect of the *P. novaehollandiae* removal on total rodent abundance can be clearly seen in Fig. 4. After the winter decline (April to 13–16 October) the control plots show the effect of a spring increase till the end of October after which there is a further decrease (dashed line, Fig. 4). However, the treatment plots show an immediate decrease following the removal (solid line, Fig. 4).

The effect of the removal on the treatment trajectory can be related to the control trajectory by making allowance for the number of *P. novaehollandiae* removed and the number of *M. musculus* that consequently immigrated. These are the

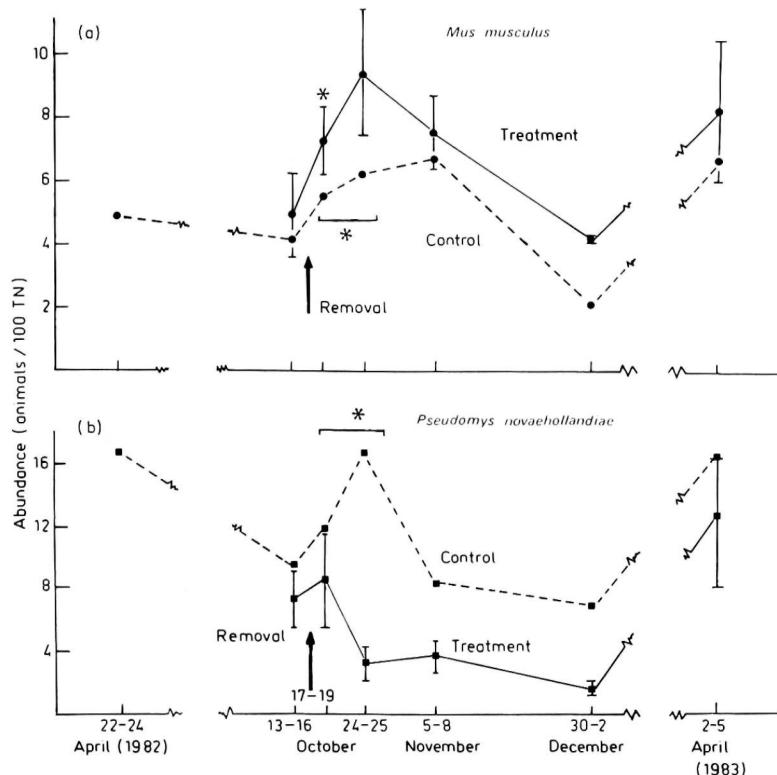


FIG. 3. The number of individual animals captured/100 TN for each trapping session shown as the mean value for control and treatment plots. Symbols as for Fig. 2. Some indications of the variation in treatment values is shown by the error bars (± 1 SEM). (a) *Mus musculus* (round symbols). (b) *Pseudomys novaehollandiae* (square symbols).

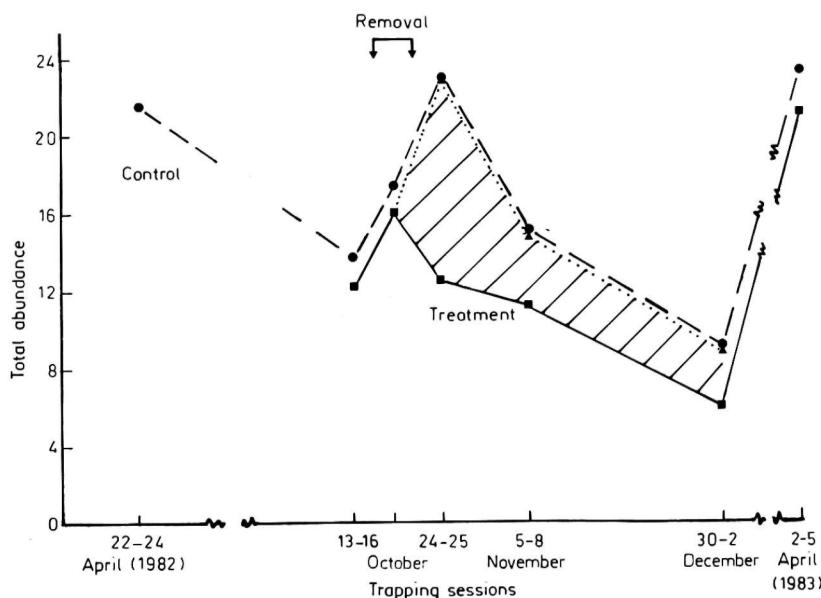


FIG. 4. The total number of individuals captured in any trapping session, for both species together. Symbols as for Fig. 2 except that the triangle and dotted line represent values for treatment plots adjusted to compensate for the perturbation of *P. novaehollandiae* removal. The hatched region represents the magnitude of the perturbation.

two simplest corrections and no further attempts are made to take account of species' differences in biomass and hence the subsequent differences in metabolic requirements. The assumption has also been made that all of the previously captured animals would be recorded in a trapping session if they were present. While a number of additional corrections might be attempted the amount of variation about such values is likely to be greater than the corrections so we have opted to adjust for the two essential corrections only. For the 24–25 October session of two days the following adjustments, can be made to the treatment abundance of 12.5 animals/100 TN, to compensate for the perturbation. The removal of 26 *P. novaehollandiae* from the four treatment plots meant that over the two nights ($4 \times 24 \times 2 = 192$ TN) the number of animals able to be captured was reduced by 13.5 animals/100 TN. However, the treatment plots showed an increase over the control plots of 3.1 *M. musculus*/100 TN, which is a response to the removal. The nett result on the treatment plots, without the perturbation would be 22.9 animals/100 TN ($12.5 + 13.5 - 3.1$), which is exactly the value found on the control plots (see dotted line, Fig. 4). Similar adjustments for the perturbation are shown for the November and December sessions, in both cases allowance is made for the overall drop in total population levels shown on the control plots [i.e. for November the effect of the 26 *P. novaehollandiae* removed is reduced by one-third because of the drop in total abundance on control plots from 22.9 to 15.1 ($7.8/22.9 = 0.34$) and the effect of the resultant increase in *M. musculus* is similarly adjusted.] The adjusted values for November and December then become 14.8 and 8.8, very close to the 15.1 and 9.0 found on the control plots. The adjustments applied to the three points joined by the dotted line in Fig. 4 are, in chronological order, + 10.4, + 3.6 and + 2.9 reflecting the attenuation of the effect of the perturbation introduced by the removal (see hatched area on Fig. 4). This can be clearly seen by the way in which the difference between treatment and control values reduces with time, so that by April it is similar to the pre-removal situation. The April 1983 value for total abundance (23.3) shows a close agreement with the other peak, in late October (22.9) and is also in agreement with the abundance found in April 1982 (21.5). This provides further evidence that the perturbation caused by the removal has not had a long term effect and that the system has returned to equilibrium.

New animals

The recruitment of new individuals into the population on each plot is shown in Fig. 5. As few juveniles were caught the recruitment appeared to be due to the immigration of adult individuals onto the plots, or alternatively the capture of previously uncaptured individuals on the plots. The latter seems less likely. The capture rates are not high enough to produce significant competition for traps making it improbable that previously uncaptured individuals would become more trappable merely because animals were removed. The only time there was an increase in the proportion of juveniles captured was for *M. musculus* during the November trapping session.

For *P. novaehollandiae* the control plots show a significant linear decrease in the number of new animals caught for the first four trapping sessions shown in Fig. 5. Treatment plots show a similar trend to control plots and there is no significant difference between them for any trapping session in the post-removal periods. *Mus musculus* also shows a decreasing trend on the control plots, though on the treatment plots the number of new animals does not continue to decrease. No single session shows a significant difference between treatment or control but the three post-removal sessions all have probabilities of 0.067. When these sessions are pooled to increase sample size the treatment plots have significantly more new animals in the post-removal periods (17–25 October and 17 October–8 November, see Fig. 5).

Introduction experiment

When the *P. novaehollandiae* were introduced to the three treatment plots (T5, T6, T7) there was considerable dispersal; of a total of 26 animals released only 14 were ever captured again. As well as emigrating from the treatment plots some animals migrated onto what was meant to be the control plot (BG1). Because *P. novaehollandiae* was captured on all four plots it was necessary to treat them all as treatment plots and rely on the two main control plots (C1 and C2) even though they were almost 1.5 km away and on an older section of the regenerating mining path.

The results of the introductions are shown in Fig. 6. No *P. novaehollandiae* had been captured on any of the four plots prior to the introductions and their abundance increased from zero to 4.0 animals/100 TN but had dropped back to 0.5/100 TN in a little

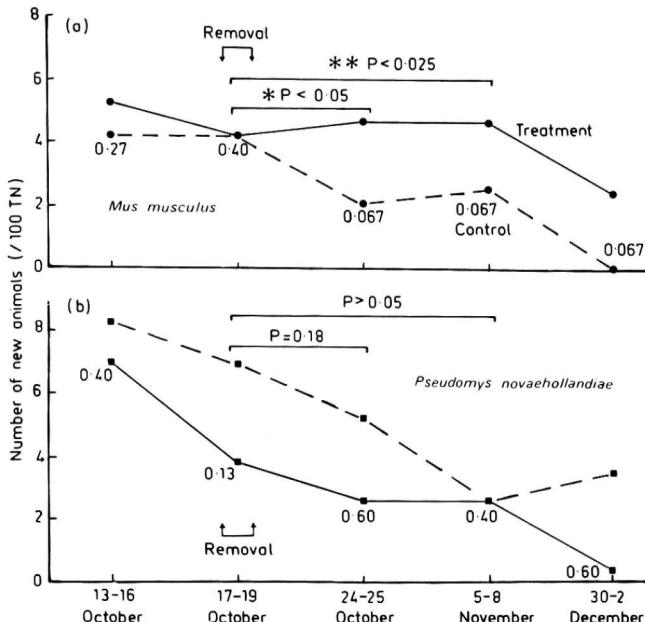


FIG. 5. The mean number of new animals caught in each trapping session, shown separately for (a) *Mus musculus* (round symbols) and (b) *P. novaehollandiae* (square symbols). Treatment plots are shown with solid lines while control plots are shown with dashed lines. Probabilities (Mann-Whitney U-test) for the difference between treatment and control values are shown for each trapping session, and significant values of single or pooled sessions are marked with stars.

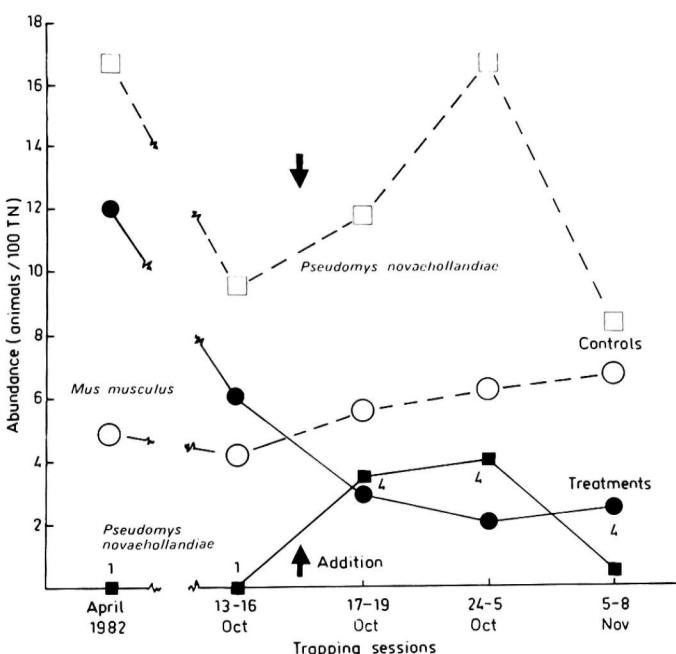


FIG. 6. The number of individual animals captured/100 TN for each trapping session for treatment plots (solid symbols and lines) and control plots (open symbols and dashed lines) in the introduction experiment. *Mus musculus* abundance is shown with round symbols and *P. novaehollandiae* abundance with square symbols.

over three weeks. In the same period *M. musculus* abundance dropped from 6.0/100 TN to 2.0/100 TN but then showed a slight increase to 2.5/100 TN. On the control plots *P. novaehollandiae* showed a similar trend, increasing then decreasing but not to such low values. However, *M. musculus* showed a continuing increase in abundance, highlighting the drop on the treatment plots. Because of the distance between control and treatment plots and the likelihood of different carrying capacities (Fox & Fox 1984) it was not valid to test for significance and it is only possible to compare the trends or relative changes rather than the absolute values.

Discussion

This removal experiment shows that the abundance of *M. musculus* on treatment plots significantly increases, relative to control plots, in response to the removal of significant numbers of *P. novaehollandiae*. These increases have been documented for the number of individuals captured per day (Fig. 2) and the number of individuals captured per session (Fig. 3).

The effects of a single pulse removal experiment are more difficult to detect than are those of multiple pulse removals. The magnitude of the perturbation is much less and the system is soon able to begin its return to equilibrium (Fig. 5). The fact that this experiment has illustrated a significant competitive effect of *P. novaehollandiae* on *M. musculus*, with a single 3-day removal, is indicative of the strength of this interspecific competition. One advantage of a single pulse removal is that it allows detection of rapid changes. The time scale encompassed in this experiment illustrates that local population changes in *M. musculus* are due to movements; rather than to changes in mortality or natality, although such changes may occur on a longer time scale. These movements may be in response to resource opportunities or to the presence of *P. novaehollandiae*.

The rate of recruitment of new animals has been used as a parameter to examine the competition between these species (Fig. 5). The use of this parameter provides additional information on the mechanism of the interaction. *P. novaehollandiae* may reduce the numbers of *M. musculus* in three ways: (a) by reducing the supply of consumable resources; (b) by direct aggression against *M. musculus*; (c) by *M. musculus* avoiding *P. novaehollandiae*.

It seems unlikely that (a) could operate sufficiently quickly, unless the resource is space *per se*. We have no direct evidence for the existence of interference competition in the form of direct aggression (b), although this does not mean it is not occurring. However, we feel that there is some indication from the responses shown that *M. musculus* avoids *P. novaehollandiae* (c) and that avoidance competition is operating. We base this interpretation on the way in which *M. musculus* appears to respond to increases in *P. novaehollandiae* abundance in a particular habitat, with dispersal out of the habitat (see the items numbered (3) and (4) in the Introduction). *Mus musculus* appears to be able to mobilize much more rapidly, to take advantage of the resource no longer being utilized because of the *P. novaehollandiae* removal. However, the longer term return to equilibrium illustrates the greater competitive ability of *P. novaehollandiae* and reflects, albeit on a more rapid time scale, the same species replacement observed in mammalian post-mining succession (Fox & Fox 1984).

The very rapid decrease in *M. musculus* abundance when *P. novaehollandiae* was introduced gives strong support for avoidance behaviour by *M. musculus* in the presence of *P. novaehollandiae*. Even though *P. novaehollandiae* illustrate their competitive superiority over *M. musculus*, with the decrease in abundance of the latter, they are unable to establish in the longer term and the introduced animals disperse from what must then be regarded as unsuitable habitat. A further trapping session on BG1 in January 1984, a period when *M. musculus* was absent from many sites while *P. novaehollandiae* was very abundant, did not reveal any *P. novaehollandiae* and only a single *M. musculus* was found from 100 TN. The use of such emigration, and immigration in the case of this experiment, is consistent with avoidance as the operable form of competition. However, it should be noted that the experiments have not been done that would prove this conclusively. As a result it is difficult to allocate the mechanism to one of Schoener's (1983) categories.

Schoener (1983) has recently reviewed field experiments on interspecific competition. Of the 164 studies he previewed, 148 showed some competition, 89% of the terrestrial studies showed competition. Schoener distinguished six kinds of competition, defined by mechanism, in an attempt at greater specificity than the exploitative and interference mechanisms of competition usually recog-

nized. Several of these categories are clearly not applicable in this study (*overgrowth* and *chemical competition*). One further category is also unlikely to be applicable, *consumptive* competition which is close to what is usually called *exploitative* competition. A fourth category of *preemptive* competition involves the passive occupancy of space and does not quite fit this study. The two final categories are *territorial* and *encounter* competition. Without more detail on how these two species interact it is not possible to confidently select one of these mechanisms. However, until we have evidence illustrating aggressive interactions between these two species we would lean towards encounter competition as the most likely contender, operating through avoidance by *M. musculus*, with the role of *P. novaehollandiae* as yet unknown as there has been no detailed work on aggression by *P. novaehollandiae*.

The fact that the total population capture rates (per 100 TN) on control plots seemed to reach similar peaks in April 1982 (21.5), October 1982 (22.9) and April 1983 (23.3), while treatment plots adjusted for the removals achieve similar levels (see Total rodent abundance), indicates there is a ceiling on rodent abundance and that this limitation is most probably caused by shortage of some resource. There are indications that space is the resource producing the competition but whether this is indirect, with the animals requiring the space for the food and burrows that it contains, or direct for the space *per se*, is not clear although we feel the indirect competition for space is more likely in this case because of the spatial niche separation shown by these two species (Fox 1980, 1981), and the fact that neither species is a specialist herbivore.

The results observed here are consistent with, and perhaps help to explain, those reported in Fox (1980). In that case not only did *M. musculus* abundance show an inverse relationship with that of *P. novaehollandiae*, but as *P. novaehollandiae* numbers increased *M. musculus* shifted out of the habitat used most by *P. novaehollandiae*. When *P. novaehollandiae* abundance decreased later, *M. musculus* returned to this 'optimal' habitat and its numbers increased. In addition the habitat niche breadth of *M. musculus* showed a significant negative correlation with *P. novaehollandiae* abundance ($r = 0.821, P < 0.05, n = 6$) (Fox 1980). However, the reciprocal correlation between *P. novaehollandiae* habitat niche breadth and *M. musculus* abundance is not significant ($r = -0.326, n = 6$). Crowell and Pimm (1976) show similar habitat shifts associated with density changes for three species of rodents on

islands off the coast of Maine.

Blaustein (1980) provides a very interesting example, supported by both field and laboratory experiments, where two subordinate species *M. musculus* and *Reithrodontomys megalotis* are only able to increase their reproductive success and use of habitat in the absence (or low abundance) of the competitively dominant *Microtus californicus*.

There is already evidence in the literature illustrating avoidance competition between small-mammal species where movement and avoidance are used to reduce aggressive encounters. A much greater incidence of avoidance rather than direct aggressive encounters was directly observed under field conditions by Congdon (1974). Hall and Lee (1982) report similar observations for *Antechinus stuartii*, *A. swainsonii* and *Rattus fuscipes*, while Braithwaite (1973) found that *R. fuscipes* acted aggressively toward *A. stuartii* and *Melomys cervinipes* in large laboratory cages, but the latter two showed avoidance of *R. fuscipes*. Evidence of reciprocal abundance and associated habitat shifts has been reported for *A. stuartii* and *Sminthopsis murina*, although there was no direct observation of avoidance behaviour (Fox 1982b).

Many studies from North America have suggested that *M. musculus* is competitively inferior to many native species. Caldwell (1964) investigated interactions between *M. musculus* and *Peromyscus polionotus* on six natural grids and a two-species field enclosure. On all six natural grids *Pe. polionotus* occurred in far greater numbers than *M. musculus*, but *M. musculus* still coexists. In the field enclosure *Pe. polionotus* increased while *M. musculus* went to extinction. Caldwell suggested that the reason for the decline of *M. musculus* in the presence of *Pe. polionotus* was that *M. musculus* was less efficient in seeking its food and did not eat the same variety of seeds as *Pe. polionotus*. Here *M. musculus* occupies an included niche and would need to be competitively superior to *Pe. polionotus* to coexist (Miller 1967). The enclosure meant that avoidance by emigration was not possible nor was recolonization by immigration possible; this lack of migration would seem to explain why *M. musculus* could coexist on natural grids but go extinct in the two-species enclosure.

Delong (1966) suggested that direct interference was the mechanism by which *Microtus californicus* displaced *M. musculus* on areas where they both occurred. Delong studied *M. musculus* populations in field enclosures in the presence and absence of *Mi. californicus*, with supplemental feeding to re-

move food as a competition factor. The rate of population increase for *M. musculus* was halved in the presence of *Mi. californicus*. Laboratory studies indicated that *Mi. californicus* caused mortality of *M. musculus* nestlings (Blaustein 1980).

Briese and Smith (1973) suggested that competition for burrow sites was the most important factor when introduction of *Pe. polionotus* caused the extinction of an established *M. musculus* population. They only found the two species coexisting on disturbed sites and suggest burning or ploughing disrupts established *Pe. polionotus* populations allowing *M. musculus* to invade and use their burrows. Their suggestion that a place to live is as important a variable as food was supported when excess food was supplied. Newsome (1969a, b) had come to the same conclusion that the availability of a place to live and adequate food were the two most important factors in the population dynamics for a population of *M. musculus* occupying reed-beds and adjacent wheat fields in South Australia.

Since Grant's classic study in 1969 the accepted way to test for interspecific competition has been to conduct manipulation experiments in enclosures [see reviews in Grant (1972, 1978)]. However, dispersal has been shown to be a major factor in interspecific competition (Caldwell 1964). Had enclosures been used in this study it may have meant a null result, as migration, apparently the major method of competition for *M. musculus*, would not have been available.

Interspecific competition and community structure

The importance of interspecific competition as a determinant of structure in small-mammal communities has been the subject of much study in North America. Brown (1975) found interspecific competition was responsible for structuring heteromyid communities in south-western deserts, M'Closkey (1976) found a similar effect in a southern Californian rodent community and then produced assembly rules for communities of four species of Sonoran desert rodents based on niche separation (M'Closkey 1978). Stamp and Ohmart (1978) reported spatial partitioning of microhabitats by Sonoran desert rodents while Price (1978) has shown that interspecific differences in foraging microhabitats are maintained by interspecific competition, in a community of the same four heteromyids, by manipulating species populations and habitat. In a very detailed study, Dueser and Shugart (1979) were able to show that microhabitat niche

pattern is related to habitat structure variables for four rodent species in a mesic forest in Tennessee and that the observed pattern is consistent with an inference of competitive coexistence.

Bowers and Brown (1982) were able to unequivocally reject the null hypothesis that granivore guilds in desert rodent communities are composed of species assembled at random with respect to body size and suggested that species of similar size coexist less frequently than expected because they are precluded by interspecific competition. Interspecific competition within guilds, but not between guilds, has been reported for a desert small-mammal community in New Mexico (Hallett 1982). For communities showing strong habitat segregation, Rosenzweig (1981) has developed a theory of habitat selection that allows competitive coexistence about an equilibrium point, with apparently no observable interspecific competition. Rosenzweig maintains that interspecific competition in the past resulted in natural selection which becomes genetically fixed, thus reducing competition. The effects of such interspecific competition would only be observable in the present by "grand perturbations of density". Schroder and Rosenzweig (1975) had already provided a field illustration of this by removing heteromyids only to find them replaced by individuals of the same species. They felt that genetically fixed habitat selection had evolved to reduce past interspecific competition. The work of Abramsky and Sella (1982) would seem to be another example of this type of community structure for gerbilline rodents in Israel. Pople (1983) has shown similar habitat selection for *P. novaehollandiae* and *M. musculus*, but this has not become genetically fixed over their interaction of less than 200 years.

In Australia, Dickman (1980, 1983) has shown by manipulation experiments that interspecific competition is an important component in an antechinus community in sclerophyll forest (*A. stuartii* and *A. swainsonii*). Other workers have also reported instances of behaviour consistent with interspecific competition between species which make up forest small-mammal communities (Braithwaite 1973; Hall & Lee 1982). Braithwaite *et al.* (1978) identified five food niches in small-mammal communities in south-eastern heaths and forests. They did not deal specifically with the role of interspecific competition in community structure. However, statements such as: "Mus musculus appeared to fill the niche of *Antechinus minimus* and partially replace *A. stuartii* and *A. flavipes* when *Antechinus* spp. were absent"; "it would appear that *A. minimus* prevents the occu-

pation of the habitat by *M. musculus*"; and "this niche may also be filled by *R. rattus* when *R. fuscipes* is absent"; would seem to indicate that interspecific competition can be important, at least for these two introduced species (*M. musculus* and *R. rattus*). Competition is more likely to be observed with introduced species where there has been too short a period for habitat selection to become genetically fixed. Dickman and Woodside (1983) have devised a simple competition model which they have tested on a three species small-mammal community in south-eastern Australia, revealing competition for space that is stronger between the two species of *Antechinus* than between the either of them and the third species (*R. fuscipes*). From their results they imply that the mechanism is interference competition.

Interspecific competition had also been claimed to be important in determining the structure of a diverse Australian small-mammal community (Fox 1980), based on indirect evidence obtained from observations of small-mammal fauna of Myall Lakes National Park (see Introduction). A test of this alternative hypothesis, against a null hypothesis of no interspecific interaction, revealed a significant effect of interspecific competition using Monte Carlo simulations for comparison with the observed field data (Fox 1981). In this case, space was the resource partitioned among species. Further indirect evidence of spatial niche separation and niche shifts between two dasyurid marsupials in the community, *A. stuartii* and *S. murina*, offered some further support for this thesis (Fox 1982b). However, the present study provides the first direct evidence of experimentally confirmed competition for space between two species making up this community. The present study also provides confirmation of the mechanism involved in the successional replacement of *M. musculus* by *P. novaehollandiae* (Fox & McKay 1981; Fox 1982b; Fox & Fox 1984). It also lends support to the habitat accommodation model of succession proposed by Fox 1982a). The failure of *P. novaehollandiae* to establish itself when transplanted to a younger section of the regenerating mining path, while at the same time illustrating its competitive superiority over *M. musculus* on older areas where they both occur, clearly fits this successional model. *Mus musculus* enters the succession following mining as soon as the habitat is suitable (within three months), *P. novaehollandiae* similarly enters the succession when the changing local physical conditions meet their specific habitat requirements. In doing so *P. novaehollandiae* dis-

place *M. musculus* by competitive superiority in the given habitat conditions (Fox 1982a; Fox & Fox 1984).

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- Addendum: See Honacki *et al.* (1982) for additional notes on taxonomy of *Mus musculus*.

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