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Movements of Feral House Mice in Agricultural Landscapes

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Abstract

From September 1992 to May 1993 we radio-collared 155 house mice (*Mus domesticus*) on agricultural fields in southern Queensland to measure movements and to determine social organisation. During the breeding season most individuals were site-attached and home ranges of both sexes overlapped extensively. There was no sign of exclusive space use for breeding individuals. Breeding males had home ranges that were larger than those of breeding females (0·035 ha *v.* 0·015 ha), and moved about more. After breeding ended, home ranges increased over tenfold in area, and most mice became nomadic and not site-attached.

Introduction

Most rodents have a polygamous mating system with a social organisation in which one sex or both are territorial (Eisenberg 1981). The house mouse is one of the most widespread rodents in the world and a serious pest in agricultural areas of south-eastern Australia. An extraordinary set of elegant experiments has been done on the social organisation of house mice in the laboratory (Lidicker 1976; Mackintosh 1978; Sage 1981; Singleton and Hay 1983) but only little has been done on social organisation in feral populations (Selander 1970; Fitzgerald *et al.* 1981; Singleton 1983). Anderson (1961) suggested that feral house mice had a social system based on territoriality of males. Breeding units were tightly defined, according to Anderson, and these units were largely closed to immigration. Justice (1962) and Myers (1974), however, could find no evidence of a territorial structuring in the feral populations they studied. Fitzgerald *et al.* (1981) found that feral house mice had a territorial social system at low density (< 3 per ha) in evergreen forests in New Zealand. Little has been done to define the social organisation of feral house mice at high densities in agricultural landscapes.

In this paper we address three questions about the movements and social organisation of house mice:

(1) do breeding house mice occupy exclusive home ranges?

(2) do movement patterns differ between breeding and non-breeding mice, and do they vary between the sexes? and

(3) do movements vary with density and among habitats in an agricultural landscape?

We have investigated these questions by the use of radio-telemetry on feral mice in agricultural fields of the Darling Downs in south-eastern Queensland.

Methods

House mice were live-trapped at seven farms on the Darling Downs, Qld, for a project on the biological control of mouse plagues (Singleton *et al.* 1995). From September 1992 to May 1993, we attached radio-collars to adult house mice on two live-trapping sites on two of these farms to obtain detailed information on movement patterns. Each trapping site consisted of a 10 × 10 grid of Longworth traps placed 10 m apart. One site (27°43′S, 151°32′E) was 2 km north of Yarranlea, and the other (27°43′S, 151°28′E) was 6·7 km west, 3 km north of Brookstead. Details of the climate, topography and habitats are presented in Singleton *et al.* (1995).

This study was restricted to one year and occurred during the generation of a mouse plague. Mouse densities began at 10–20 per ha in September 1992 and grew exponentially to over 500 per ha in June 1993. The breeding season had already begun by September 1992 and extended into April 1993. The mouse plague collapsed rapidly in June and July 1993 so that by early July it was nearly impossible to capture a single individual to radio-collar. Because of this rapid crash we were unable to obtain more data on individuals in the non-breeding season.

Live trapping sites were located at the edges of agricultural fields and included a grass verge 5–10 m wide at one edge. Two crops per year are grown in the Darling Downs and adjoining agricultural fields were planted to wheat or barley (winter), sorghum (summer), or left fallow.

We measured movements during five study periods from September 1992 to May 1993. Each study period lasted 7–10 days, and we radio-collared 22–37 individuals in each period. We put radio-collars on all adult-sized mice (> 15 g or 80 mm head–body length) we caught during the first day or two of live trapping. When excess individuals were available, we collared the largest individuals in all the available habitats. There were virtually no recaptures between trapping sessions and no individual was ever radio-collared twice.

We used AVM model SM1, Titley model LT1 and Biotrack model SS2 radio-transmitters and, after unsuccessful attempts to attach transmitters to the back using skin glues, we used cable ties to attach transmitters around the necks of the mice. These transmitters weighed 0·7–1·4 g (4–8% of body weight) and their batteries lasted 5–14 days. Radio-tracking sessions were of necessity short-term because of this limitation. We did three radio-fixes each evening between 1800 and 2300 hours and one additional fix in the morning, so that potentially we could obtain 4 locations per day for each individual. When radio-collared individuals disappeared we searched for them on foot within 1 km of the live-trapping areas. During our checks we failed to locate 1·7% of the individuals known to be alive, so that most radio-collars that disappeared were presumably due to animal movements, predation or radio-failure rather than our poor searching abilities. Searches, however, could never be complete because, although we could pick up most radios at 50–100 m distance, radio-collars that had their whip antenna chewed off had only a 10–15-m range. We also used an all-terrain vehicle to cover a larger search area, and in March 1993 Gordon Grigg used a fixed-wing aircraft to search for missing radio-collars over several kilometres around the study zone.

We studied movement patterns for adult mice only, and we classified mice as breeding if males had descended testes and if females were lactating or had a perforate vaginal orifice. Extensive concurrent autopsies of house mice from the same areas confirmed that mice of these sizes were in breeding condition (Singleton, unpublished data).

Movement patterns and home ranges were analysed by the use of RANGES IV (Kenward 1987). Statistical analyses were carried out with SYSTAT (Wilkinson 1988).

Results

Measures of Home Range

Two classes of home-range models seem most appropriate for feral house mice in agricultural landscapes: polygon models and non-parametric utilisation distribution models (Worton 1987). Polygon models provide the outer boundary of the area used, while utilisation distributions attempt to specify the usage pattern within the home range. The incremental area plot of mononuclear polygons for 49 house mice that were located 20 or more times is shown in Fig. 1. In many cases home ranges were well defined after 10 fixes, but some individuals with larger ranges required more than 20 fixes to define their area of use. We discarded all individuals located fewer than 10 times. Above this cutoff line (10) there is for our data no correlation between the number of locations and the estimated size of the home range ($r = 0{\cdot}07$, $n = 107$, $P > 0{\cdot}60$).

Spearman's coefficients of rank correlation among various measures of home-range size are given in Table 1. We calculated mononuclear convex polygons covering 100% and 95% of the observed points, and used the Kernel estimator of Worton (1989) for 100% and 95% of the observed data. All these methods provide highly correlated estimates for home ranges (Table 1), so that little advantage accrues to the use of the more complex Kernel estimators. This may reflect the limitation of having only 10–30 data points for range estimation for our animals. We have therefore decided to analyse space use by means of 95% mononuclear convex polygons. Some individuals have occasional movements that are far outside their normal range, and for this reason we prefer 95% polygons over 100% polygons. We have completed all of the subsequent analyses using all the different measures of home range and our conclusions are robust to this decision to present only 95% polygons.

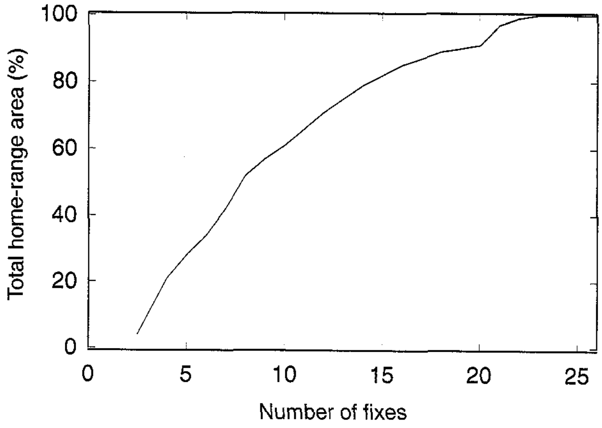

Fig. 1. Incremental area plot for 95% convex polygon home ranges of 49 house mice with 20–30 fixes, Darling Downs, Qld.

Table 1. Spearman's coefficients of rank correlation among five measures of space use in feral house mice on the Darling Downs

n = 107. All animals had 10–30 locations. Distance between successive locations measured linearly. $P < 0{\cdot}001$ for all coefficients

	Mononuclear polygons		Kernel analysis		Distance
	95%	100%	95%	100%	between locations
100% convex polygons	0·92	1·00			
95% Kernel	0·96	0·94	1·00		
100% Kernel	0·89	0·98	0·94	1·00	
Distance	0·86	0·91	0·91	0·94	1·00

Home-range Size

The distribution of home-range sizes in feral house mice is highly skewed. For 94 mice measured during the breeding period from September 1992 to March 1993, 95% polygons range from 0·0009 to 3·012 ha, with a mean of 0·15 ha and a median of 0·01 ha (10 m by 10 m). The majority of mice have home ranges less than 0·02 ha during the breeding season (Fig. 2). Home ranges were ln-transformed to reduce the skewed distribution for statistical analysis.

We took four samples during the breeding season (September, November, February and March) and used ANOVA to test for the effect of sex, breeding condition and month on home-range size (95% polygons). A preliminary analysis of covariance showed that sample size (number of locations) was not a significant covariate ($P = 0{\cdot}87$) and explained almost none of the variance in home-range size, so we deleted sample size from the analysis. Our ANOVA ($n = 94$) was unbalanced and we could not estimate the second-order interaction. There were no significant first-order interactions and neither breeding condition ($P = 0{\cdot}64$) nor month ($P = 0{\cdot}32$) were significant first-order effects. The only significant factor was sex ($P = 0{\cdot}047$). Home ranges of males averaged 0·035 ha (*c.* 19 by 19 m) (95% confidence limits 0·020–0·058, transformed from log), and home ranges of females averaged 0·015 ha (*c.* 12 by 12 m) (0·009–0·025 ha, 95% c.l.). Box plots (Fig. 3) show the considerable overlap in home-range size for the two sexes during the breeding season.

In contrast to the remarkable lack of significant effects during the breeding season, home ranges differed dramatically between the breeding and the non-breeding periods. Unfortunately, we have only one sample of 13 mice post-breeding (May); however, in a two-way ANOVA of sex and season, season is highly significant ($P = 0{\cdot}002$) (Fig. 4). The median home range was 0·014 ha during the breeding season and 0·199 ha in the non-breeding season, over ten times larger. There was no detectable effect of sex ($P = 0{\cdot}48$) or any interaction of sex and season ($P = 0{\cdot}55$) in the analysis. Home-range size did not change with population density in these agricultural fields over a large range of densities (10–600 per ha).

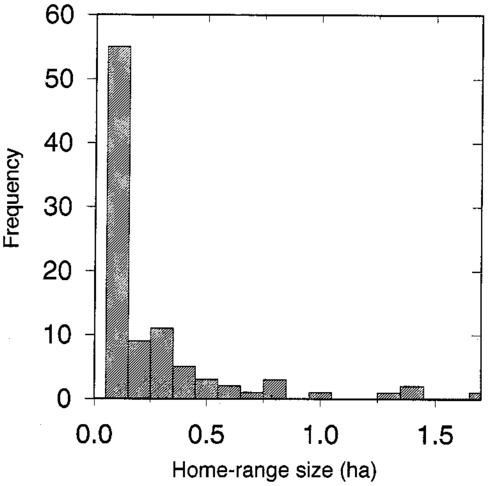

Fig. 2. Frequency plot of home-range sizes (mononuclear 95% ranges) for both male and female house mice during the breeding season ($n = 94$). The range size (ha) axis is logarithmic. The majority of mice have home ranges less than 0·02 ha in area.

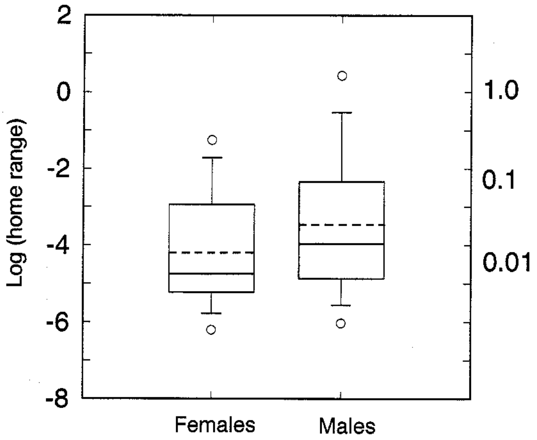

Fig. 3. Box plot of mononuclear 95% convex polygon home-range sizes (ha) for male and female house mice during the breeding season, September 1992 to March 1993. The box encloses the 25th and 75th percentiles, the solid line shows the median and the dotted line the mean home-range size. Vertical lines span the 10–90th percentiles, and circles give the extreme values. All data ln-transformed. The right-scale values give actual home ranges in ha. $n = 56$ males, $n = 38$ females.

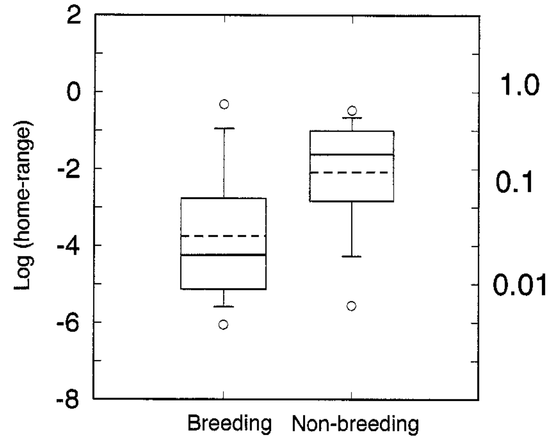

Fig. 4. Box plot of mononuclear 95% convex polygon home-range sizes (ha) for house mice from the breeding period (September–March) and the non-breeding period (May). Vertical lines span the 10–90th percentiles, and circles give the extreme values. $n = 94$ breeding, $n = 13$ non-breeding.

Home-range Overlap

We have no direct observations on house mice in our study and the only way to begin to assess space use in these rodents is to see whether there is overlap in the use of space on a short time scale. If breeding males are strongly territorial, we expect minimal overlap in space use, and the same prediction can be applied to breeding females. If, however, there is substantial overlap in space use by breeding adults, we could have a social system based on dominance hierarchy or a territorial system in which subordinates are tolerated within the territory of the dominant animal. These predictions follow directly from the type of social organisation found in laboratory studies of the house mouse (Crowcroft 1955; DeLong 1978; Singleton and Hay 1983). One problem with testing for overlap with our data is that we were not able to radio-collar all the breeding mice on our study areas. In spring we attached radio-collars to nearly all the adult males on the study area and most of the adult females, but in summer when densities exceeded 100 per ha we could radio-collar only 15–30% of the breeding mice. We can at best conduct an asymmetric test with minimal overlap estimation. If we find a high degree of overlap, we can reject the simple territorial model. On the other hand, if we find little overlap, we cannot be certain that there is still little overlap with unmarked animals.

Home-range overlaps were calculated on mononuclear 95% polygons because these types of home ranges would show minimal overlap (compared with utilisation distributions estimated with Kernel analysis). During the breeding season home-range overlap occurred on 26% of home ranges of males (based on 582 potential overlaps) and 19% of home ranges of females (based on 208 potential overlaps). The frequency distribution of overlaps for home ranges of males is illustrated in Fig. 5. On average when home ranges of males overlap, 31% of the ranges are overlapping, but the critical factor is that a large number of breeding male mice were recorded with home ranges overlapping 90–100%. One set of home ranges for breeding male mice in November 1992 with extensive overlap is illustrated in Fig. 6. We conclude from these data that neither male nor female house mice show any pattern of exclusive space use during the breeding season in these agricultural landscapes. Home-range overlap occurred equally at low and at high mouse densities.

One explanation for extensive home-range overlap is that there is social grouping and the social group defends a group territory. We cannot discount this model of social organisation for our populations but there was no evidence from our home-range maps that several individuals had coincidental home-range boundaries.

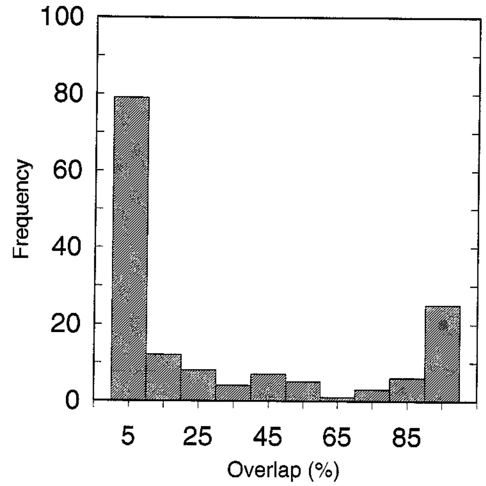

Fig. 5. Frequency distribution of percentage overlap of ranges for adult male house mice during the breeding season ($n = 150$). Home ranges were measured as 95% convex polygons. Note the substantial number of home ranges with 90–100% overlap. Not all adult males on the study area could be radio-collared and thus the lack of overlap is not meaningful.

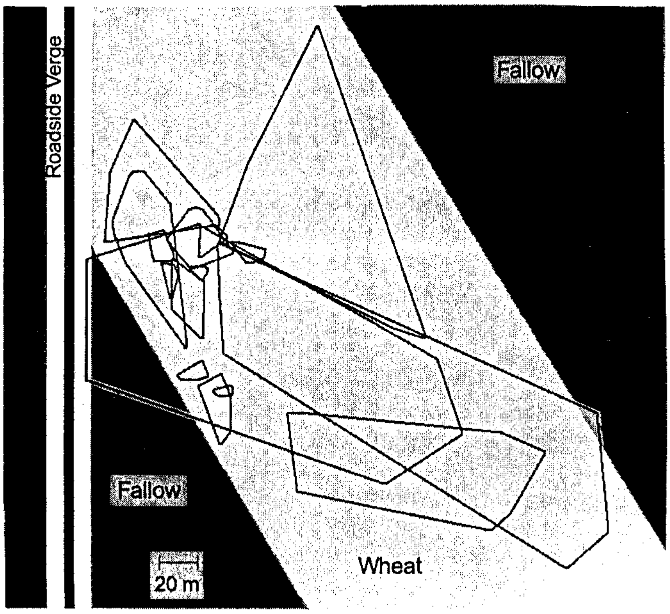

Fig. 6. Home ranges of 18 breeding male house mice on one plot in spring, 4 November 1992. A total of 23 breeding males were estimated to be on this plot at this time. All these males were in breeding condition, and yet there is extensive overlap of home ranges measured by radio-locations over a 1-week period. Home ranges are 95% convex polygons.

Habitat Use

Social organisation might be habitat specific in house mice. Newsome (1969*a*, 1969*b*, 1970) suggested that mice in permanent habitats form a donor population with a stable organisation and export juveniles and subadults to recipient habitats. In our study, permanent habitats were represented only by roadside grass verges 5–10 m in width. If there is a stable group of mice in these verge habitats we would expect to have a higher recapture rate for adults caught in verges and a reduced movement rate.

Since we had relatively few mice that were radio-collared in verge habitats, we combined all four samples from the breeding period. We ran an ANOVA with sex and habitat (verge, non-verge) as the factors, using mononuclear 95% convex polygons as a measure of home-range size. Sex was a significant main effect ($P = 0{\cdot}01$) and habitat was not ($P = 0{\cdot}36$), but the sex-by-habitat interaction was nearly significant ($P = 0{\cdot}076$). The interaction means and confidence limits are given in Table 2. Verge-inhabiting females move much less than females in more unstable habitats (crops) and males in verges move much more than other males. Breeding males collared in verge habitat have home ranges ten times the size of breeding females in verges, while in other habitat the sexes differ by only 55% in average home-range size (Fig. 3).

Table 2. Mononuclear 95% convex polygon home ranges for breeding house mice from verge and non-verge (crop) habitats, data pooled from September to March

Home ranges were transformed back from logarithms after the ANOVA was run. CI, confidence interval

Habitat	Sex	Mean home range (ha)	95% CI	Sample size
Verge	Female	0·004	0·002–0·008	5
	Male	0·046	0·008–0·282	9
Crop	Female	0·019	0·011– 0·032	33
	Male	0·029	0·017– 0·049	47

Discussion

There are four major models of social organisation in feral house mice. Model I, proposed by Anderson (1961), is that feral mice at low-to-medium density have a territorial social organisation in which home ranges of breeding males are wholly exclusive and home ranges of breeding females are often exclusive as well. Established territories would be closed to immigration and most juveniles would emigrate from their natal range in this model. Model II, proposed by Newsome (1969*a*), is that feral house mice are not territorial but show social dominance dictated largely by body size. There is no territorial defence in either sex in this model, although there is site-attachment. Emigration is one consequence of social dominance, and immigration is always possible, subject to dominance relations. Model III, proposed by Justice (1962), is that feral house mice have no social organisation but are nomadic. Individuals are not site-attached (except for females for litter production). Dominance is transient and interactions typically non-aggressive. Wounding of breeding animals would be predicted to be highest in Model I and lowest in Model III. Model IV is that feral house mice have a clan structure in which several reproductive individuals might occur in any one clan.

Field evidence from both observational data on feral populations (DeLong 1967; Newsome 1969*b*; Stickel 1979; Singleton 1989) and from genetic substructuring of feral populations (Myers 1974; Baker 1981; Singleton and Redhead 1990) has been mostly against Model I. The exception is the careful study of Fitzgerald *et al.* (1981) on feral house mice in evergreen forests in New Zealand. These New Zealand populations were at low density (0·5–3·3 per ha) and there was a strong indication of exclusive space use in both sexes and indications of territorial defence. Our study provides evidence against exclusive space use for house mice at high density in agricultural landscapes, and thus is more consistent with Model II than with Model I. Model III is not applicable to feral house mice in the breeding season but does appear to operate in the non-breeding period, at least at high densities (Krebs *et al.* 1994). Newsome (1969*b*) found house mice to be nomadic in wheatfields in dry summers but to be resident and to breed in wet summers. Model II is the model consistent with most field studies of house mice during the breeding period. Breeding mice are site-attached but do not occupy exclusive areas.

The view that house mice live in isolated demes or closed social groups has been widely held since the early work by Anderson (1961). Baker (1981) showed that new alleles could spread rapidly between social groups of house mice living in chicken coops and that social groups were not as tightly organised as Anderson (1961) suggested. Singleton (1983) found tight social structuring in house mice in zoo aviaries but pointed out that these demes had a short lifespan and consequently there was a continual mixing of the gene pool. The importance of dispersal of juvenile mice in gene flow has been suggested by these studies but there are few direct data on dispersal rates or dispersal distances in feral house mice.

Our findings in this study are consistent with general ideas about social organisation in other animals (Emlen and Oring 1977; Krebs and Davies 1991). During the breeding season high-quality food is not in short supply in agricultural areas of the Darling Downs (Bomford 1985). For males the limiting resource at this time is breeding females, and for females the limiting resource is a safe site to raise their litters. The role of infanticide in feral house mouse populations is largely unknown. Adult rodents of both sexes can be infanticidal, but in most laboratory studies adult females caused the major losses (Labov *et al.* 1985). If infanticide occurs in feral *Mus* populations, females ought to defend a territory around their nest. Strong territorial defence by pregnant or lactating females has been reported in laboratory studies (Crowcroft and Rowe 1963; Reimer and Petras 1967; Lidicker 1976; Singleton and Hay 1983). Our observations are not sufficiently detailed to determine whether there is nest-defence territoriality in lactating females, and this could well repay further study in the field.

Feral house mice may not correspond to all the predictions of Ostfeld's (1985) models of territoriality in microtine rodents. Female *Mus* with superabundant food should not be territorial, according to Ostfeld (1985). However, Ostfeld (1985) predicts that when females are not territorial, males should be. If the lack of territoriality of males is caused by intruder pressure, we would expect to find males becoming territorial in low-density *Mus* populations. There has been no clear sign of territorial space use by males of most feral populations (Newsome 1969*b*; Myers 1974) but the question deserves more detailed study using both radio-telemetry and direct observations. Fitzgerald *et al.* (1981) found territorial social organisation in house mice at low density. Redhead (1982) suggested that males held individual territories at low density and group territories at higher densities during the breeding period. We have not detected such a switch in social organisation at the densities observed in our study (5–500 per ha).

Home-range sizes of house mice recorded in this study are within the range of observations summarised in Sage (1981, p. 70) but only one-tenth of the size recorded by Fitzgerald *et al.* (1981). Most individuals occupied an area of 0·01–0·02 ha during the week of radio-tracking. Whether these home ranges may shift over time spans longer than one week is not known. Stickel (1979) found evidence of one large-scale exodus of established mice from a hay field into a maturing wheat field at the start of the spring breeding season.

Caldwell (1964) and Newsome (1969*b*) suggested that house mice might be subdivided into residents and transients that differ in their movements and social pattern. The definition of transient as an individual caught only once in live-traps may be confounded by low trappability and social status. We need an independent method for determining transients as a social group. Krebs *et al.* (1994) estimated that a maximum of 21% of radio-collared individuals might be transients during the breeding season, and more likely only half or less of these were transients. In this study a transient was defined as an individual that never remained within the same 100 m radius for two days, and never returned to the original capture point. The vast majority of mice caught during the breeding period were probably residents in all these feral populations.

During the non-breeding period our data (Krebs *et al.* 1994) suggest that house mice switch to a nomadic type of social organisation (Model III). The proximate cause of this switch is probably food shortage and a lack of cover, and both the lack of breeding and this social change are consequences of a deteriorating food situation after agricultural crops like sorghum have been harvested (Bomford and Redhead 1987). It is this switch to nomadic behaviour that may produce the typical plague syndrome described by Newsome (1969*a*), Redhead (1982) and Singleton (1989).

If feral house mice in agricultural landscapes switch from a territorial social organisation at low density to one based on social dominance at high density, it is important to find out exactly how this occurs and at what density. Fitzgerald *et al.* (1981) reviewed all the studies of feral house mice and suggested that home-range size declined with density below about 50–100 mice per ha, but above this level home-range size was nearly constant. Anderson (1961) suggested this same density range for the transition from territoriality to social hierarchies. This could be the range of density to investigate for a switch in social organisation. Territorial social systems provide the best prerequisites for social regulation of population changes in rodents (e.g. Labov *et al.* 1985). If social aggression in house mice is highly heritable, as found by Singleton and Hay (1982), there could be natural selection for or against aggression as population density changes in these feral agricultural populations. This switch in social organisation could be just a consequence of the density changes or it could be a cause contributing to the release of populations from social regulation to then increase to plague proportions.

Acknowledgments

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References

Anderson, P. K. (1961). Density, social structure, and nonsocial environment in house-mouse populations and the implications for regulation of numbers. *Transactions of the New York Academy of Sciences, Series II* **23**, 447–51.

Baker, A. E. M. (1981). Gene flow in house mice: introduction of a new allele into free-living populations. *Evolution* **35**, 243–58.

Bomford, M. (1985). Food quality, diet and reproduction of house mice on irrigated cereal farms. Ph. D. Thesis, Department of Zoology, Australian National University, Canberra.

Bomford, M., and Redhead, T. (1987). A field experiment to examine the effects of food quality and population density on reproduction of wild house mice. *Oikos* **48**, 304–11.

Caldwell, L. D. (1964). An investigation of competition in natural populations of mice. *Journal of Mammalogy* **45**, 12–30.

Crowcroft, P. (1955). Territoriality in wild house mice (*Mus musculus* L.). *Journal of Mammalogy* **36**, 299–301.

Crowcroft, P., and Rowe, F. P. (1963). Social organisation and territorial behaviour in the wild house mouse (*Mus musculus* L.). *Proceedings of the Zoological Society of London* **140**, 517–31.

DeLong, K. T. (1967). Population ecology of feral house mice. *Ecology* **48**, 611–34.

DeLong, K. T. (1978). The effect of the manipulation of social structure on reproduction in house mice. *Ecology* **59**, 922–33.

Eisenberg, J. F. (1981). 'The Mammalian Radiations: An Analysis of Trends in Evolution, Adaptation, and Behavior.' (University of Chicago Press: Chicago.)

Emlen, S. T., and Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science* **197**, 215–23.

Fitzgerald, B. M., Karl, B. J., and Moller, H. (1981). Spatial organisation and ecology of a sparse population of house mice (*Mus musculus*) in a New Zealand forest. *Journal of Animal Ecology* **50**, 489–518.

Justice, K. E. (1962). 'Ecological and Genetical Studies of Evolutionary Forces acting on Desert Populations of *Mus musculus*.' (Arizona–Sonora Desert Museum: Tucson, Arizona.)

Kenward, R. (1987). 'Wildlife Radio Tagging.' (Academic Press: London.)

Krebs, C. J., Singleton, G. R., and Kenney, A. J. (1994). Six reasons why feral house mouse populations might have low recapture rates. *Wildlife Research* **21**, 559–67.

Krebs, J. R., and Davies, N. B. (1991). 'Behavioural Ecology: An Evolutionary Approach.' (Blackwell Scientific Publications: Oxford.)

Labov, J. B., Huck, U. W., Elwood, R. W., and Brooks, R. J. (1985). Current problems in the study of infanticidal behavior of rodents. *Quarterly Review of Biology* **60**, 1–20.

Lidicker, W. Z. (1976). Social behaviour and density regulation in house mice living in large enclosures. *Journal of Animal Ecology* **45**, 677–97.

Mackintosh, J. H. (1978). The experimental analysis of overcrowding. In 'Population Control by Social Behaviour'. (Eds F. J. Ebling and D. M. Stoddart.) pp. 157–80. (Institute of Biology: London.)

Myers, J. H. (1974). Genetic and social structure of feral house mouse populations on Grizzly Island, California. *Ecology* **55**, 747–59.

Newsome, A. E. (1969*a*). A population study of house-mice permanently inhabiting a reed-bed in South Australia. *Journal of Animal Ecology* **38**, 361–77.

Newsome, A. E. (1969*b*). A population study of house-mice temporarily inhabiting a South Australian wheatfield. *Journal of Animal Ecology* **38**, 341–59.

Newsome, A. E. (1970). An experimental attempt to produce a mouse plague. *Journal of Animal Ecology* **39**, 299–311.

Ostfeld, R. S. (1985). Limiting resources and territoriality in microtine rodents. *American Naturalist* **126**, 1–15.

Redhead, T. D. (1982). Reproduction, growth and population dynamics of house mice in irrigated and non-irrigated cereal farms in New South Wales. Ph. D. Thesis, Department of Zoology, Australian National University, Canberra.

Reimer, J. D., and Petras, M. L. (1967). Breeding structure of the house mouse, *Mus musculus*, in a population cage. *Journal of Mammalogy* **48**, 88–99.

Sage, R. D. (1981). Wild mice. In 'The Mouse in Biomedical Research, Vol. I: History, Genetics, and Wild Mice'. (Eds H. L. Foster, J. D. Small and J. G. Fox.) pp. 39–90. (Academic Press: New York.)

Selander, R. K. (1970). Behavior and genetic variation in natural populations. *American Zoologist* **10**, 53–66.

Singleton, G. R. (1983). The social and genetic structure of a natural colony of house mice, *Mus musculus*, at Healesville Wildlife Sanctuary. *Australian Journal of Zoology* **31**, 155–66.

Singleton, G. R. (1989). Population dynamics of an outbreak of house mice (*Mus domesticus*) in the mallee wheatlands of Australia — hypothesis of plague formation. *Journal of Zoology (London)* **219**, 495–515.

Singleton, G. R., and Hay, D. A. (1982). A genetic study of male social aggression in wild and laboratory mice. *Behavior Genetics* **12**, 435–48.

Singleton, G. R., and Hay, D. A. (1983). The effect of social organisation on reproductive success and gene flow in colonies of wild house mice, *Mus musculus*. *Behavioral Ecology and Sociobiology* **12**, 49–56.

Singleton, G. R., and Redhead, T. D. (1990). Structure and biology of house mouse populations that plague irregularly: an evolutionary perspective. *Biological Journal of the Linnean Society* **41**, 285–300.

Singleton, G. R., Spratt, D. M., and Chambers, L. K. (1995). An experimental field study to examine whether *Capillaria hepatica* (Nematoda) can limit house mouse populations below plague densities in eastern Australia. *Wildlife Research* **22**, 31–53.

Stickel, L. F. (1979). Population ecology of house mice in unstable habitats. *Journal of Animal Ecology* **48**, 871–87.

Wilkinson, L. (1988). 'SYSTAT: The System for Statistics.' (Systat Inc.: Evanston, Illinois.)

Worton, B. J. (1987). A review of models of home range for animal movement. *Ecological Modelling* **38**, 277–98.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**, 164–8.

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