

MOVEMENTS AND SOCIAL ORGANIZATION OF WILD HOUSE MICE (*MUS DOMESTICUS*) IN THE WHEATLANDS OF NORTHWESTERN VICTORIA, AUSTRALIA

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From September 1996 to May 1997, 187 wild house mice (*Mus domesticus*) were fitted with radiotransmitters at an agricultural site in the wheatlands of northwestern Victoria, Australia, to examine movements and social organization. Males had slightly larger home-range areas than females. Home-range size was highly variable (0.0002–8.024 ha) but could not be predicted from body size or body condition in males and females, or by whether females were breeding. Mice were site-attached during the breeding season, with extensive intersexual overlap of home ranges but variable intrasexual overlap. Home ranges were significantly larger during the nonbreeding season compared with the breeding season. Evidence existed for exclusive home-range use by females at all densities of mice, low to moderate home-range overlap for males when densities were low and increasing, and an apparent switch to a more gregarious phase in male mice when the breeding season ceased and densities were high. Nonbreeding mice seemed to be nomadic when densities were low, which is consistent with an earlier study of home ranges and social organization of mice on the Darling Downs, Queensland.

Key words: agricultural landscape, house mouse, movements, *Mus domesticus*, radiotelemetry, social organization

The house mouse (*Mus domesticus*) is a significant pest in the grain-growing regions of eastern and southern Australia because of the ability of this rodent to form outbreaks reaching 1,000 mice/ha (commonly referred to as mouse plagues). Current approaches for controlling this pest include poisoning (Brown et al. 1997; Kay et al. 1994; Mutze 1993; Twigg et al. 1991) and habitat manipulation (Singleton 1997). The potential use of a virally vectored immunocontraceptive incorporated into an overall integrated control strategy also is under investigation (Chambers et al. 1997). These approaches require an understanding of movement patterns and social organization

of mice in an agricultural context. Although studies have examined social organization in the laboratory (e.g., Butler 1980; Crowcroft and Rowe 1963; Singleton and Hay 1983) and in outdoor enclosures (e.g., Lidicker 1976; Noyes et al. 1982; Wolff 1985), few studies have examined movements, habitat use, and social organization of feral house mouse populations (Fitzgerald et al. 1981; Krebs et al. 1995b; Newsome 1969a, 1969b; Selander 1970; Singleton 1983).

Krebs et al. (1995a) argued that social factors might regulate mouse populations at low densities; disruption of social regulation could be a necessary condition for the generation of a plague. They proposed 2 alternative models on how social behavior

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could regulate mouse populations and favored 1 of those for agricultural landscapes in Australia. That model postulated a nomadic social system at low population densities, strongly territorial behavior during population increases, and finally a breakdown of territorial behavior when densities were high. We predict that if the above model is true, a radiotelemetry study of a house-mouse population at varying densities should show a high number of lost signals or long-range movements of mice at low densities, little intrasexual overlap in home-range areas as population density increases (i.e., during the breeding season), and extensive overlapping of home-range areas at high densities.

Only 1 study has attempted to define the social organization of house mice in agricultural landscapes in Australia using radiotelemetry (Krebs et al. 1995b). That study found that during the breeding season most individuals demonstrated site fidelity with extensive overlap of home ranges. Breeding males had larger home ranges and were more active than breeding females. After breeding ceased, home ranges increased more than 10-fold, and most mice became nomadic.

We examined home-range sizes and the extent and degree of home-range overlap of house mice in a cereal-growing region in northwestern Victoria, Australia, during increasing mouse abundance. We tested null hypotheses that for breeding and nonbreeding seasons of mice no difference existed in the extent or degree of home-range overlap, no difference existed in home-range size, and no difference existed in the proportion of lost signals. We also examined body size and body condition in males and females and female breeding condition as predictors of home-range size.

MATERIALS AND METHODS

Study site.—Our study was carried out on a farm 8 km S of Walpeup in northwestern Victoria (61°07'S, 142°01'E) from September 1996 to May 1997. The crop regime, soil type, and

climate for that area were described by Singleton and Chambers (1996). A narrow ephemeral channel (about 2 m wide), providing water to nearby dams for 2 months of the year, formed the northern border of the site. Alongside this channel was a grassy strip varying from 5 to 30 m in width. A 2nd grassy strip (5 m wide) was associated with a fenceline bordering the west of the site. Grasses provided dense cover in these strips in September but began seeding and dying off in October and November, respectively. From December to May, vegetative cover along fencelines was sparse and dry. Barley and wheat were grown on the eastern side of the fenceline. They were at a vegetative stage at the beginning of the study, flowered in October, and matured by November. The crop was harvested in December, leaving stubble about 0.4 m in height. This stubble was grazed by sheep for the rest of the study. To the west of the fenceline was pasture. A 0.3-ha patch of sparse *Eucalyptus* (mainly *E. largiflorens*, *E. camaldulensis*, *E. aggregata*, and *E. viminalis*) woodland with tall wheatgrass (*Agropyron elongatum*) understory was present on a seepage area within the crop. *Eucalyptus* displayed the distinctive multi-stemmed growth form typical of vegetation in this region (Parkes and Cheal 1990).

Collection of demographic data.—Mice were live-trapped for 2–4 nights before each tracking session using Longworth single-capture traps. Traps were set 10 m apart in grass strips alongside the channel and fencelines and around the woodland. A 5 by 5 grid was set in the woodland and a 7 by 7 grid was set in the barley crop. Trapping effort ranged from 287 trap nights to 725 trap nights each session depending on mouse abundance. Each mouse was individually marked using a Hauptner brass ear tag (Sieper & Co., Sydney, Australia), weighed (± 0.1 g), and measured (head–body length, ± 1.0 mm), and reproductive condition was assessed for females (Singleton 1983). Individual body condition was calculated from the regression equation of Krebs and Singleton (1993), discounting pregnant females. Breeding season was confirmed from autopsies of females trapped on nearby sites each month.

Barrier fence.—In September–December, a barrier fence was constructed around the woodland and grass areas where mice were trapped before tracking. This fence was built to maximize captures and attempt a total enumeration

of the population in those habitats, a requirement for analysis of range overlap between individuals. The fence was constructed of 200 μm by 0.9 m by 50 m lengths of plastic dug in at the base to a depth of 0.10 m. The plastic was supported by medium tensile, Flexibel[®] fencing wire (Hall Rural Centre, Canberra, Australia) held at a height of about 0.7 m by fencing posts spaced at 5-m intervals. The top 0.05–0.10 m of plastic was folded over the top of the wire and secured with packing tape. When trapping was completed and tracking of mice was in progress, the plastic was folded away from the wire fencing and covered with soil. When mouse numbers were high in January–May 1997, the barrier fence was not used because enumeration of the population was not possible because of a high rate of trap occupancy by mice.

Radiotelemetry.—We used single-stage transmitters (Sirtrack, Havelock North, New Zealand) attached to a cable tie that functioned as a radiocollar around the neck of the mouse. Only adult mice >75 mm or >13 g were tracked. The weight of a transmitter (1.2–1.4 g) was about 8–9% of the average body weight of mice with collars ($X = 15.6$ g). Battery life of transmitters was 12–15 days, restricting each tracking session to 5–10 days.

Between 13 and 29 animals were radiocolored (average 24) in each of 8 sessions between September 1996 and May 1997. We attempted to fit transmitters to an equal number of males and females during each session, but this was not achieved in September, January, April, and May because few large adult females were caught. When animals of suitable size were in excess of the number of collars available, those caught along the grass areas and within the woodland were given priority over those caught in the cropland. This was done to minimize tracking of transient mice and measure home ranges of residents that had burrow sites in the grass and woodland habitats. Eight animals were tracked on more than 1 occasion: 6 of them twice and 1 each for 3 and 4 times, respectively.

Potentially 4 radiolocations were obtained each day, 3 each night between 1800 and 0100 h and once during the day. All fixes were separated by at least 1 h. All animals were tracked on foot using a handheld 3-element Yagi antenna and TR4 (Sirtrack, Havelock North, New Zealand), TR2 (Biotrack, Dorset, United Kingdom), or Regal 2000 (Titley Electronics, Ballina, Aus-

tralia) receivers. More than 80% of animals could be tracked to ≤ 1 m of their actual location. Signals that could not be detected were searched for on foot within ≤ 1 -km radius of the last known location.

Analyses.—Home-range analyses were performed using RANGES V (Kenward and Hodder 1996). Krebs et al. (1995b) identified polygon models and nonparametric utilization–distribution models as the most appropriate for examining movements of wild mice. We calculated mononuclear convex polygons covering 100% and 95% of the observed points and the Kernel estimator for 100% and 95% of the observed data (Worton 1989). Home-range sizes using those methods were compared using Spearman's rank correlation analysis and were highly correlated (all $r_s = 0.81$ – 1.00 , $n = 139$, $P < 0.001$ for all coefficients). Therefore, we used the simpler 95% convex polygon home ranges for subsequent analyses.

Home-range overlap was calculated during the breeding and nonbreeding seasons for males and females and was presented as the percentage of overlapping ranges from the number of potential overlaps. Potential overlaps were the number of possible combinations of overlapping individuals (e.g., if 5 individuals were tracked, there were 20 potential overlaps). Degree of overlap (as a percentage of the total home-range size) was calculated for overlapping males during the breeding season. Regression analysis was used to determine if home-range size could be predicted by body size or body condition of mice.

Population abundance was estimated as the number of mice caught per 100 trap nights, adjusted using Caughley's (1977) density–frequency transformation. The proportion of females breeding was based on the number of females lactating or pregnant (determined by palpation) divided by the number of adult females (>72 mm). Two-way analysis of variance was used to test for effects of sex (male versus female) and breeding season (breeding versus nonbreeding) on home-range size (95% polygons).

RESULTS

Based on autopsy data, mice began breeding in August and weaned the last litter for the season around mid-April. In early September, 14 of 25 adult females were

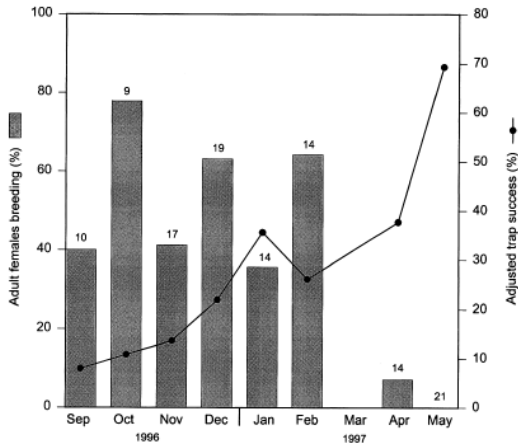


FIG. 1.—Percent adjusted trap success (line) and percentage of adult female house mice pregnant or lactating (bars) in the wheatlands of northwestern Victoria, Australia. Numbers above each bar are sample sizes.

pregnant (5 were 3rd trimester), and 12 of 25 had recent placental scars and were lactating. In the last week of February, 8 of 14 adult females were pregnant (4 in 1st trimester), and by early April, no mice were pregnant ($n = 20$).

Results of livetrapping indicated that breeding activity peaked in October 1996 when 80% of females caught were either lactating or pregnant (Fig. 1). From September to February, 40–60% of females were breeding. In April, only 7% of females caught were breeding (all lactating), and therefore all males had ceased mating. Thus, our study had 7 tracking sessions during the breeding season (September–April) and 1 during the nonbreeding season (May).

Mouse abundance increased from 8% trap success to 69% trap success from September 1996 to May 1997 (Fig. 1). That was equivalent to about 15–420 mice/ha (G. Singleton, in litt.). When the plastic barrier fences were in place, 66% (range, 50–87%) of captures were recaptures from the previous night(s). Without the fence, number of recaptures dropped to 16% (range, 10–29%). Of the large mice caught in the

grass and woodland, 63–100% were fitted with transmitters at any 1 session.

Of 187 mice fitted with transmitters, 159 (85%) were tracked throughout their tracking session; however, 139 of those were used in analyses of home range. Twenty mice died before a sufficient number of fixes could be obtained based on an incremental area plot of number of fixes versus the cumulative home-range area. That plot indicated that about 60% of the home range was defined after 12 fixes, and that had increased to about 90% by 22 fixes. We included only mice with >12 locations ($n = 139$); most of those (78% of the 139 used in the analyses) had ≥ 20 locations defining their home range. Movements and trap sites of the other 48 mice, and their proximity to mice with home ranges used in the formal analyses, were noted.

For 40 mice whose location was unknown at the completion of the tracking session, 22 (55%) mice dropped their transmitter and 18 (45%) mice had undetectable radio signals. Twelve of the 40 mice had their home-range area estimated, because >12 fixes were obtained before the animal was lost. However, home ranges for those mice may have been underestimated. Percentage of signals lost per tracking session was highest in October (23%), April (14%), and May (17%), but otherwise was generally low (4–11%). When the signal was lost, it was not known whether the animal had left the area or the radio had failed. Of 25 mice (13%) that died during tracking, 7 deaths were known to occur from predation by snakes or raptors. Five of the 25 mice were still included in the analyses because >12 fixes were obtained.

Frequency of home-range sizes was highly skewed (Fig. 2), and varied from 0.0002 to 8.024 ha, with a mean of 0.271 ha and a median of 0.04 ha. Using log-transformed estimates, home-range size did not differ between males and females ($F = 3.465$, $d.f. = 1, 135$, $P = 0.065$). However, the P value was close to the 0.05 level of significance, suggesting that male home ranges were

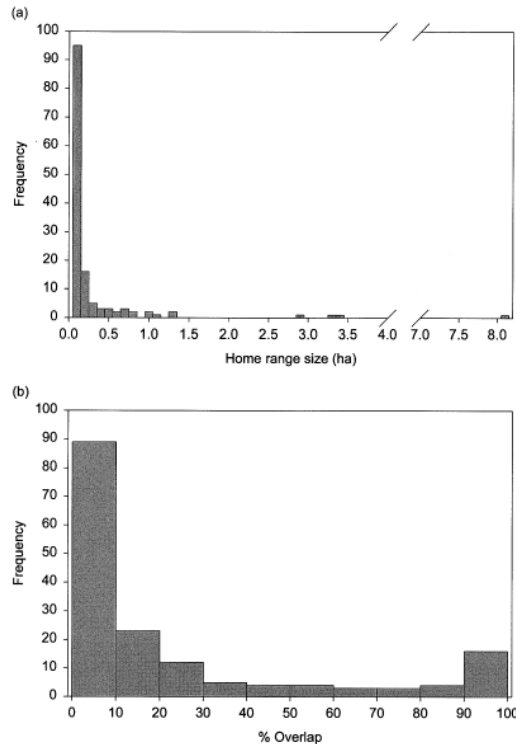


FIG. 2.—Frequency plots of a) home-range sizes (95% convex polygons) for male and female house mice ($n = 139$) and b) degree of overlap (as a percentage of home-range area) between adult male house mice with overlapping home ranges during the breeding season ($n = 159$ overlaps).

slightly larger than those of females. Home ranges were significantly larger for mice tracked during the nonbreeding season compared with the breeding season ($F = 4.018$, $d.f. = 1, 135$, $P = 0.047$). No differences occurred among home ranges of lactating, pregnant, or nonbreeding females ($F = 0.099$, $d.f. = 2, 45$, $P = 0.91$). Further, home-range size did not increase with increasing body size ($r^2 = 0.004$, $n = 137$, $P = 0.483$) or body condition ($r^2 = 0.002$, $n = 130$, $P = 0.620$) for males and females combined.

During the breeding season, 18% of males had home ranges that overlapped with other males (based on 906 potential

overlaps), but overlap generally was small (0–10% of the home range; Fig. 2). On average, when home ranges of males overlapped, 23% of the area was shared. For each tracking session, percentage of home ranges overlapping ranged from 0% to 25% (September, December, January, and May; Fig. 3). During the nonbreeding season when mouse densities were at their peak for this study, the percentage of male home ranges overlapping increased to 57% (based on 132 potential overlaps; Fig. 3), but the degree of overlap remained similar to that observed during the breeding season.

For females, 13% had overlapping home ranges during the breeding season (based on 262 potential overlaps), and no overlap was observed for females during the nonbreeding season (based on 20 potential overlaps). The degree of overlap between females was generally less than that observed for males (65% overlapped by <10%), and only 1 instance of 90–100% overlap was found between individual home ranges. For each tracking session, percentage of home ranges overlapping ranged from 0% to 27% (September, December, January, and May; Fig. 3). In all months, home ranges of males and females overlapped (Fig. 3).

Eight animals were tracked more than once (2–4 sessions). Each animal was tracked in a similar location at each tracking session, with 21–57% of their home ranges from different trapping sessions overlapping. No consistent trend of increasing or decreasing home-range size was found between consecutive sessions.

Animals fitted with radiotransmitters, but not used in the analyses of home-range area and overlap, supported trends observed in degree of home-range overlaps. Numbers of animals in that category for each month from September to May were 5, 2, 4, 5, 1, 6, 13, and 12, respectively (total = 48). The few movements or initial trap locations for those individuals showed exclusive intrasexual spatial use. Six individuals from the April and May tracking sessions showed

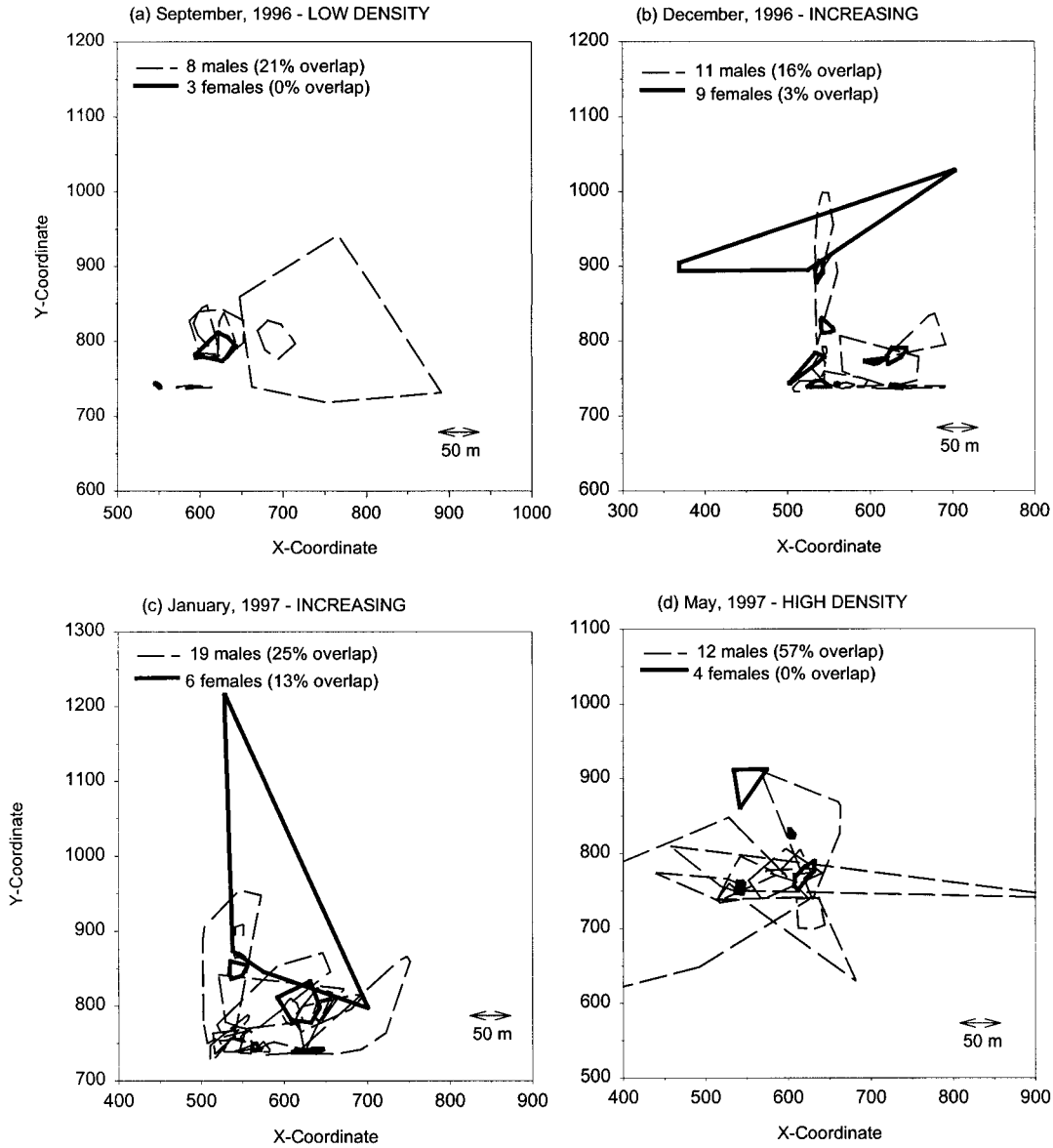


FIG. 3.—Home-range plots (95% convex polygon areas) for all house mice radiotracked in a–c) 3 months during the breeding season, and d) 1 month during the nonbreeding season. During the a) September and b) December tracking sessions, a barrier fence was used to enumerate the population before tracking but was not used in c) January or d) May. Percent overlap is the number of ranges overlapping divided by the number of potential overlaps multiplied by 100. Low Density, Increasing, and High Density refer to abundance of mice at the site at each tracking session.

long-range movements of 300–1,000 m, with an additional 12 individuals either dropping their transmitter or with locations unknown because of loss of signal.

DISCUSSION

Home-range areas for house mice throughout this 9-month study were consis-

TABLE 1.—Summary of mouse home-range data in northwestern Victoria, Australia (present study) and on the Darling Downs, Queensland (Krebs et al. 1994, 1995b). Sites were about 1,500 km apart and had markedly different farming systems. Pe = Petersen estimate of number of mice per hectare; TS = trap success per 100 trap nights adjusted using Caughley's density–frequency transformation (Caughley 1977).

	Darling Downs	Northwestern Victoria
Home range data		
Males versus females	Males > females	Males ≥ females
Frequency distribution	Highly positively skewed	Highly positively skewed
Median home-range size		
Breeding	0.014 ha (<i>n</i> = 94)	0.037 ha (<i>n</i> = 122)
Nonbreeding	0.199 ha (<i>n</i> = 13)	0.119 ha (<i>n</i> = 17)
Range overlap	Extensive intra- and intersexual overlap	Extensive intersexual overlap; variable intrasexual overlap
Breeding season versus nonbreeding season	10 times increase in home-range size during nonbreeding season compared with breeding season	3 times increase in home-range size during nonbreeding compared with breeding season
Breeding condition	No effect on home-range size	No effect on home-range size
Potential nomadism	Breeding season = 30% nomadic; nonbreeding season = 66% nomadic	Breeding season = 8% nomadic; nonbreeding = 17% nomadic
Density dependent	No; range of mouse densities = 10–500 (Pe), or 25–325 (TS)	No; range of mouse densities = 15–260 (Pe), or 10–70 (TS)
Farming system	Winter and summer crops; heavy clay soils; predominantly summer rainfall; no fences	Winter crops only; light sandy soils; predominantly winter rainfall; fences

tent with those obtained by Krebs et al. (1995b) in mouse populations on a cereal farm on the Darling Downs in southeastern Queensland (about 1,500 km from Walpeup; Table 1). Home ranges were <0.1 ha for 68% of mice and <0.01 ha for 21% of mice. Similar home-range areas also have been measured during a radiotelemetry study of *Mus spretus* in grassland in Portugal (Gray et al. 1998).

For males, intrasexual home-range overlap varied between breeding and nonbreeding seasons, and, therefore, between increasing and high-density populations (Fig. 1). Percentage of home ranges overlapping was low to moderate in the breeding season. In the nonbreeding season, males showed an apparent switch to a more gregarious phase, with 57% of ranges overlapping. No such difference was found for female mice: high exclusive use of home

ranges occurred consistently throughout the study.

To examine the extent and degree of overlap between home-range areas, and in particular to detect if animals are territorial, requires that a significant proportion of the population is tracked during each tracking session. In our study, we attempted to capture all individuals in the study area when population density was low by using a plastic barrier fence during trapping to contain the population. The proportion of recaptures to new captures on the last night of each trapping session indicated that we were close to achieving this. When barrier fences were in place (September–December), 66% of captures were recaptures and 63–100% of mice weighing >13 g were fitted with transmitters. Therefore, the low percentage (average 14% for males and females) of intrasexual home-range overlap

from September to December, the period when a large proportion of the adult population was caught and tracked, suggests that mice may have had a territorial social organization at this time.

Without the fence, from January onward, number of recaptures dropped to 16%, suggesting that the proportion of the population trapped was low and that our estimates of home-range overlap were conservative. The location of individuals for which we had <12 locations supported our conclusions of exclusive intrasexual home-range use during the breeding season and long-range movements during the nonbreeding season.

These results support the suggestion that male mice have high behavioral plasticity, ranging from strongly territorial behavior to gregarious social groups (Redhead 1982). However, our results contrast with studies that indicate that mice maintain territorial behavior for most of the year (Anderson 1961; Fitzgerald et al. 1981; Selander 1970). The potential for mice to form gregarious units is consistent with the high densities observed during mouse plagues in the grain-growing regions of Australia (Singleton and Redhead 1990).

Our study supports predictions of the model proposed by Krebs et al. (1995a) for mice in Australian agricultural landscapes. Evidence was found of nomadism at low density (23% of signals were lost in October) and after the breeding season ceased in May (17% of signals lost). Home-range overlap for males also was low to moderate during the breeding season (18%) when the population was increasing, but overlap rose to 57% after the population ceased breeding and densities were high. This contrasts with the Darling Downs study (Krebs et al. 1994) where mice were relatively nomadic, regardless of density and breeding season (Table 1). Such results emphasize the need to examine social structure of mice in field populations at a finer scale (Gray et al. 1998). In particular, little is known of social organization during the nonbreeding season (both our study and that by Krebs et al.

[1995b] had only 1 tracking session during the nonbreeding season), or the influence that social behavior has on the dispersal of young. For example, will territorial behavior result in presaturation dispersal of young mice (Lidicker 1975) and therefore play an important role in how mice use the dynamic mosaic of agricultural ecosystems?

Determining the underlying social structure of mouse populations in agricultural landscapes is crucial to developing and implementing an effective management strategy. For example, virally vectored immunocontraception has been identified as a promising control technique for house mice in Australia (Chambers et al. 1997; Shellam 1994; Singleton 1994). Social organization will influence the rate of spread of a virally vectored sterilizing agent through the direct inter- and intrasexual interactions between males and females and indirect effects on dispersion or retention of young mice at their natal site (Lambin 1994; Lambin and Krebs 1991; Lambin and Yoccoz 1998; Wolff 1992). Although the former may be examined using radiotelemetry, the latter is difficult to quantify under field conditions. Use of radioisotopes to follow movements of neonates from their mother's home range is a possible technique (Tamarin et al. 1983), but may not be permitted in cropland.

One problem when working with an outbreaking species such as house mice is that temporal replication in a study such as this is difficult. We probably would have to wait a further 5–7 years for similar population dynamics, given that this is the average time between outbreaks in southern Australia (Singleton and Redhead 1989). During most of 1997 and 1998 after our study was completed, capture rates of <5 mice/1,000 trap nights were the norm, with traps distributed over a much larger area than used in our study (G. R. Singleton, in litt.). This is typical of mouse densities in the interim between outbreaks (Pech et al. 1999). Therefore, to replicate a study such as this temporally is not a trivial exercise. We sug-

gest that a further radiotelemetry study at a similar stage of house-mouse population dynamics would be beneficial to test the generality of our results.

A similar drawback is the difficulty of spatial replication. Given the considerable resources required to radiotrack a significant proportion of the population at 1 site, as we have attempted here, it was not possible for us to examine movements of mice at more than 1 site. However, the similarity in results obtained by this study and the earlier study by Krebs et al. (1995b), about 1,500 km away, suggests that results may be generally applicable to cereal-growing regions of southern and eastern Australia. Further studies are encouraged to test this hypothesis.

With radiotelemetry studies, the risk always exists that the presence of the radio will somehow hinder movements of the animals and negatively bias home-range sizes. In the present study, we tracked 8 individuals on more than 1 occasion. In all cases, mice were retrapped in the areas where they had been originally radiotracked, suggesting that movements observed while animals were carrying transmitters were representative of their true home range. This is consistent with laboratory and field trials of effects of transmitters on wild mice, which have indicated that movements, survival, and dominance status are unaffected by a transmitter (Pouliquen et al. 1990).

Our study in the wheatlands of north-western Victoria provided evidence that mice tend toward exclusive intrasexual home ranges when mouse populations are breeding and at low density, particularly for females. Males become gregarious and home ranges increase in size as mouse densities increase and the breeding season ends. The high proportion of lost radio signals in April and May also suggests that mice may have more nomadic movement patterns during the start of the nonbreeding season. Because of the paucity of information obtained during the nonbreeding season on mouse social behavior in field pop-

ulations, a detailed radiotelemetry study is required for a better understanding of the social organization of mice in cereal-growing regions of eastern Australia.

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