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Six Reasons Why Feral House Mouse Populations Might Have Low Recapture Rates

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Abstract

Many feral house mouse populations have low recapture rates (0–20%) in live-trapping studies carried out at 2–4-week intervals. We consider six hypotheses to explain low recapture rates. We radio-collared 155 house mice between September 1992 and May 1993 in agricultural fields on the Darling Downs of south-eastern Queensland during a phase of population increase. Low recapture rates during the breeding season were due to low trappability and during the non-breeding period to nomadic movements. During the breeding season radio-collared mice of both sexes survived well and moved mostly small distances (<11 m). Low trappability has consequences for the precision of population indices that rely on catch per unit effort. Capture–recapture models robust to heterogeneity of trap responses should be used to census feral *Mus* populations.

Introduction

One of the most characteristic features of mark–recapture studies of feral house mice (*Mus domesticus*) is that there is a very low recapture rate of marked individuals. While similar studies of voles and mice have recapture rates of 60–100% when samples are taken every few weeks (Krebs and Boonstra 1984), for feral house mouse populations recapture rates of 0–20% are the norm. Singleton (1987) reported recapture rates of 11–20% for Longworth live-traps at monthly intervals. In southern Queensland Willliams and Wilson (1980) found only 19% of 2253 tagged mice were caught one month later. Newsome *et al.* (1976) found recapture rates of 16% for feral house mice in California. Why should recapture rates be so low?

One simple explanation would be that house mice have much higher rates of reproduction and mortality than other rodents of similar size, so that population turnover is more rapid. This explanation can be rejected at the outset because the house mouse is a typical rodent in its reproductive schedule, maturing at 4–6 weeks of age with a 19–21-day gestation period, a 21-day lactation period, and a litter size of 4–10 (Berry 1981). House mouse populations in Australia can increase at rates of population growth (r-values) of 0·10 per week (Singleton 1989; Cantrill 1992), rates of population growth that are within the range shown by vole and lemming populations in the Northern Hemisphere (Krebs and Myers 1974). We can therefore reject the rapid-turnover hypothesis.

Low recapture rates could also result from the disturbances that are inherent in modern agriculture. This could be a possible explanation only if the agricultural disturbances associated with harvesting and planting occurred more frequently than live-trapping sessions. This is not the case for any of the studies discussed here, which are based on live-trapping at 3–6-week intervals. We do not think that agricultural disturbances can explain these low recapture rates.

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There are six possible explanations for low recapture rates in house mice, as follows.

(i) *Low trappability.* House mice could avoid live-traps at all times or only after their first capture, and this type of poor catchability might explain the low recapture rates.

(ii) *Study areas too small.* If the live-trapping area is too small, edge effects overwhelm the mark–recapture data. If most individuals in the study area spend most of their time in other parts of their home ranges, recapture rates would be low.

(iii) *Nomadic social organisation.* If house mice do not live in defined home ranges but wander as nomads in agricultural landscapes, a low rate of recaptures would be expected on a fixed live-trapping grid.

(iv) *Trap saturation.* If the density of house mice is several orders of magnitude more than is conventionally believed, trap saturation would be the rule and low recapture rates would be observed. This is similar to but not identical with the first explanation involving low trappability.

(v) *High death rates of marked mice.* If marked animals are affected by tagging and handling such that they often die or expose themselves to natural hazards, the recapture rate would be low.

(vi) *High emigration rates of marked mice.* One alternative to the previous mechanism would be for marked animals to move away from their home range, possibly because of the trauma associated with trapping.

One or more of these explanations must be correct, and the next step is to list the predictions of each hypothesis. The predicted observations for each hypothesis are shown in Table 1. By radio-collaring individual mice we can determine trappability directly and also measure the survival rate of individuals that are caught and handled. If mice are moving long distances, we should observe movements between adjacent live-trapping grids and large movements of radio-collared mice. By estimating population density with alternative, non–box-trapping methods [e.g. pitfalls (Singleton 1987) or radiotelemetry], we should be able to determine whether true densities are much higher than those estimated from live-trapping with Longworth box traps. Finally, since females must raise their litters at fixed locations for a minimum of three weeks, adult female trappability must be higher than male trappability during the breeding season for a purely nomadic model of social organisation.

Table 1. Predictions of six hypotheses to explain low recapture rates in feral house mouse populations

Hypothesis	Radio-collared animals remain in home range	Radio-collared animals survive well	Observed movements very large	Alternative indices of density high	Sex difference in trappability
1. Low trappability	Yes	Yes	No	No	No
2. Small area	Yes	Yes	Yes	No	No
3. Nomadic	No	Yes	Yes	No	Yes[A]
4. Trap saturation	Yes	Yes	No	Yes	No
5. High death rate	No	No	No	No	No
6. High emigration rate	No	Yes	Yes[B]	No	No

[A] During breeding season females must be site-attached for lactation period.
[B] Marked mice only.

Each hypothesis gives a unique set of predictions in Table 1. Complications could arise if more than one of these hypotheses is functioning, but we will begin our analysis by looking at a single-factor explanation for low recapture rates.

Methods

House mice were live-trapped at seven farms on the Darling Downs, Queensland, for a project on the biological control of mouse plagues (Singleton and McCallum 1990; Singleton *et al.* 1995). From September 1992 to May 1993 we attached radio-collars to adult house mice at two live-trapping sites on two of these farms to obtain detailed information on movement patterns. We used AVM model SM1, Titley model LT1 and Biotrack model SS2 radio-transmitters and, after unsuccessful attempts to attach transmitters to the back with skin glues, we used cable ties to attach transmitters around the necks of the mice. These transmitters weighed 0·7–1·4 g (4–10% of body weight) and their batteries lasted 5–14 days in the field. Radio-tracking sessions were necessarily short term because of this limitation set by battery life. When radio-collared individuals disappeared we searched for them on foot within 1 km of the live-trapping areas. Searches could never be complete because, although we could pick up most radios at 50–100 m distance, radios 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 a fixed-wing aircraft was used to search for missing radios over several kilometres around the study zone.

We do not know whether the radio-collars affected survival or trappability of the mice. Because the enlarged part of the collar was placed underneath the chin, there was no physical barrier to entering a live-trap. There was no obvious large reduction in survival in our study animals, but we do not have an independent means of testing for survival effects from radio-collaring house mice.

Live-trapping procedures utilised standard grid trapping with Longworth live-traps. Trapping grids were 10×10 checkerboards with 10-m trap spacing. One hundred Longworth live-traps were placed on each grid. The two grids used for radio-tracking were 7 km apart. Grids were live-trapped for four nights on average (range 2–9) during a trapping session. The trapping procedures are described in detail in Singleton (1989). Survival rates were estimated from radio-collared mice by means of the staggered-entry design of Pollock *et al.* (1989).

Results and Discussion

The available data on survival and residency of house mice that were radio-collared are summarised in Table 2. On average one-third of the mice collared disappeared within three days. There are three possible fates for these mice. First, they could have moved more than 300 m off the trapping area and not returned. Such individuals we call 'nomadic'. Second, predators may have killed the mice and carried them beyond our detection zone. Third, radios could have failed for technical reasons, and mice could still be alive on the trapping area. We think that, of these three possibilities, radio failure is the least important and nomadic movement is the most important contributor to these disappearances. This belief is based on the following reasoning. Of all the radios connected, 10% failed in the first day or two of life, before they could be put on mice in the field. Because most of these failures are associated with soldering faults in these tiny radios, we expect most failures to occur quickly, before the radios are set out on mice. This belief could be tested with a set of unused radios but we have not been able to afford such a test.

Predator kills are more difficult to evaluate as a source of loss. We have picked up 17 kills in the course of this study. Most of these were probably raptor kills, and all were found within 200 m of the trapping grids. We have observed Australian kestrels (*Falco cenchroides*), black-shouldered kites (*Elanus notatus*), pied butcherbirds (*Cracticus nigrogularis*) and Australian magpies (*Gymnorhina tibicen*) catching house mice, and they nearly always stopped to eat the mouse within a short distance of the capture point. Kestrels and kites did not damage the radios but removed the radio collar from the carcass before eating the mouse. We found two kills that appeared to be due to red foxes and one kill probably due to a house cat. It is possible that predators do carry off mice with radios but we think that this sort of loss is small. If the predator kill rate was as high as our radio loss rate, these mouse populations would be extinct rather than increasing rapidly.

Nomadic movements appear to be the major reason why one-third of our radios disappeared within three days of tagging. Particularly in dry weather in May, after breeding

Table 2. Survival and movements of radio-collared house mice on the Darling Downs, Queensland, during 1992–1993

Time	Crop, stage	No. mice collared	No. mice tracked for >3 days	No. mice possibly moving long distances[A]	No. known to move long distances[B]	No. known to remain on home range[C]	Survival rate of residents[D] per 14 days
Males							
Sep. 1992	Barley, maturing	14	10	4	1	9	1·00
Nov. 1992	Wheat, maturing	20	17	3	3	14	0·90
	Barley, stubble	1	1	0	0	1	1·00
Dec. 1992	Wheat, harvesting	6	4	2	0	4	1·00
	Barley, stubble	6	4	2	0	4	1·00
Mar. 1993	Sorghum, stubble	11	10	1	1	9	0·53
	Sorghum, maturing	7	6	1	2	4	0·49
	Wheat, ploughed stubble	4	4	0	0	4	1·00
May 1993[E]	Sorghum, stubble	19	8	11	0	8	0·56
Total (breeding season only, Sep.–Mar.)		**69**	**56**	**13 (19%)**	**7 (10%)**	**49 (71%)**	**0·75 (mean)**
Females							
Sept. 1992	Barley, maturing	8	5	3	0	5	1·00
Nov. 1992	Wheat, maturing	2	2	0	0	2	0·09
	Barley, stubble	4	3	1	0	3	1·00
Dec. 1992	Wheat, harvesting	9	7	2	0	7	1·00
	Barley, stubble	6	4	2	0	4	0·44
Mar. 1993	Sorghum, stubble	11	10	1	0	10	1·00
	Sorghum, maturing	4	3	1	1	2	0·57
	Wheat, ploughed stubble	5	3	2	0	3	1·00
May 1993[E]	Sorghum, stubble	18	5	13	2	3	0·62
Totals (breeding season only)		**49**	**37**	**12 (24%)**	**1 (2%)**	**36 (73%)**	**0·69 (mean)**

[A] Radio signal lost within three days after collaring; fate unknown.
[B] Moving more than 100 m from original capture site and staying there more than two days.
[C] Remaining at least three days on home range.
[D] Estimated following Pollock *et al.* (1989), assuming all disappearing individuals represent censored observations.
[E] Non-breeding season.

had largely stopped, nearly two-thirds of the collared mice disappeared immediately. For a few of these individuals we were able to track directional movements away from the point of capture for 1–2 days until we lost contact with them. There was a significant difference in nomadism between the breeding and non-breeding periods for both sexes (χ^2 tests, $P < 0{\cdot}005$). On average, a maximum of 21% of individuals were potentially nomadic during the breeding season (September–March), assuming all the lost radios were due to nomadic movements, and males appeared to move longer distances more often than females. During the non-breeding period in May, 65% of individuals were potentially nomadic. We must therefore separate the breeding and non-breeding periods to evaluate the hypotheses in Table 1.

During the breeding season, 71–73% of adult house mice that were radio-collared remained on their home range throughout the radio-tracking period, and their survival rate was relatively high (Table 2). These are minimal estimates of residency, and we note that they apply only for the 7–10-day period of radio-transmission. If we assume, for illustration, that 28% of adult mice emigrate every 10 days, we would still expect to find 37% of adults tagged after one month, twice the recovery rate that Singleton (1987) reported. If emigration occurred at this scale, we would expect to capture tagged mice on adjacent live-trapping grids. This rarely occurred in our study, and Twigg *et al.* (1991) also reported no dispersal between grids. These observations eliminate three hypotheses in Table 1—the high death rate, high emigration rate, and nomadic models—for the breeding period.

The trap-saturation model seems unlikely to be the explanation for low trappability for house mice on the Darling Downs. In this study traps became saturated after January 1993 because of population increase, and we had three trapping periods with excess traps in September, October and November 1992 and three trapping periods with trap saturation in January, February and May 1993. In spite of this, the probability of capture per day for individual mice was 0·15 for the periods with excess traps ($n = 8$) and 0·13 for the periods with trap saturation ($n = 9$), a non-significant difference. A second reason to reject the trap-saturation model is that population densities of house mice do not seem to be several orders of magnitude higher than is conventionally believed, unless all the available data on survival rates, litter size, and rate of population increase are faulty. The isopleths of the instantaneous rate of population change (r, per week) for house mice, as a function of adult survival rate and reproductive rate, are shown in Fig. 1. This is an oversimplified life-table for the breeding season. It assumes a litter size of 7·4 (Singleton and Redhead 1990) and sexual maturity for females at 5 weeks (Drickamer 1987). Fig. 1 can be used to judge the internal consistency of rates of increase for house mouse outbreaks. For example, Singleton (1989) estimated a 10-fold increase during a mouse plague in the Victorian mallee in six months in 1983–84 ($r = 0{\cdot}09$ per week), and a survival rate of 0·66–0·70 per two weeks. Fig. 1 shows that these rates are consistent with a recruitment rate of 6·5–7 juveniles per pregnancy, which indicates virtually no loss in the nest or early juvenile stages. Note that the recruitment rate in Fig. 1 is an aggregate measure of litter size, pre-weaning mortality in the nest, and early post-weaning losses. If house mouse densities were much higher than the conventional methods of population estimation suggest, these life-table calculations would not balance. Also, from September to December recapture rates were low in this study, even with a great excess of live-traps available. Cantrill (1992) estimated average rates of population growth of $r = 0{\cdot}082$ per week for house mice on the Darling Downs, a rate of increase nearly identical to that obtained by Singleton (1989) for the Victorian mallee.

We are left with two possible explanations for low recapture rates: low trappability and small study areas. During the breeding season the average distance moved between capture points or radio-locations was 5–10 m (Krebs *et al.* unpublished data). Population density in this study increased rapidly from 10–20 mice ha^{-1} in September 1992 to about 700 ha^{-1}

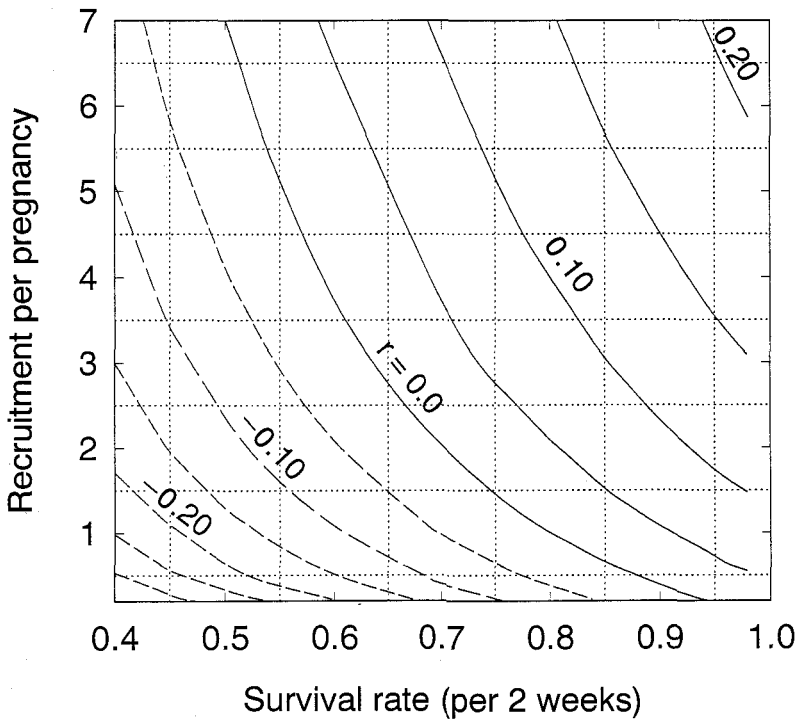

Fig. 1. Isopleths of the instantaneous rate of population growth (r) per week for a hypothetical house mouse population subject to a constant adult survival rate and a constant recruitment rate (young produced per pregnancy). Continuous breeding after five weeks of age and a litter size of 7·4 are assumed. These isopleths are likely to represent a maximal rate of population growth for feral mice.

in May 1993. There was no significant change in movements as density increased (Krebs *et al.* unpublished data). These movements are similar to those reported for other feral house mouse populations (e.g. DeLong 1967; Newsome 1970; Sage 1981; Newsome *et al.* 1982). Twigg *et al.* (1991), for example, reported a mean distance moved of 10·9 m in soybean crops in New South Wales. These observations are at variance with the small-area hypothesis, and we conclude that with 1-ha trapping grids we should be able to recapture individuals readily.

Low recapture rates of feral house mice during the breeding season seem to be due to low trappability. The simplest explanation for low trappability is that, when food is available in excess in the vicinity of the live-traps, individual mice rarely enter traps. Since our live-traps have only food (wheat) in them, there is little or no trap attraction as shelter. In many agricultural landscapes food is in excess supply for a large part of the year. If this explanation for low recapture rates is correct, we would predict that trappability will be higher in more stable, food-poor environments and that trappability will change dramatically some time after harvest when grain supplies are depleted. In most of the wheatbelt of eastern Australia the winter is a time of relative food shortage, and consequently we would predict higher trappability in winter for the non-nomadic sector of the mouse population. On the Darling Downs, where two agricultural crops are produced each year, the timing of relative food shortage may vary with the cropping pattern used on individual farms.

We have anecdotal data to support the prediction of higher trappability when food is short, from live-trapping to recover radio collars on the Darling Downs. At the end of our 7–10-day radio-tracking session we would find the exact burrow a radio-collared mouse occupied and set 3–5 Longworth live-traps outside the burrow entrance. From September to March we had poor success in retrapping these specific individuals, and on average we estimated the chance of capturing a mouse to be only about 20% even when we knew the exact burrow location. Throughout this time there was a vast surplus of wheat, barley and sorghum seed available to mice. In May, by contrast, two months after harvest, seed was in relatively short supply and we re-trapped all our radio-collared mice ($n = 7$) without problems, often within an hour of setting the live-traps. The suggestion that low trappability in house mice is a product of excess food availability is consistent with these observations.

An alternative suggestion from the work of Newsome (1969) is that shelter availability dictates trappability in house mice. There is an association in our work between periods of low trappability and extensive soil-cracking in the clay soils of our study area from September to March (median probability of capture per day = 0·11), and higher trappability in May when fewer soil cracks were available (median probability of capture = 0·29). Newsome (1966) also found in laboratory tests that house mice were harder to trap the second time than the first, and this short-term effect could compound other influences on trappability.

General Discussion

The most important consequence of the fact that house mice in agricultural landscapes have low recapture rates is that population parameters are more difficult to estimate. Much of the analysis of house mouse population dynamics in Australia relies on the assumption that catch per trap night is a reliable index of density (Redhead 1982; Bomford and Redhead 1987; Singleton 1989). Newsome (1969) separated residents and nomads in his trap catch to estimate density but again these techniques assume that trappability of residents is high. Analysis of mouse plagues in which density varies over four orders of magnitude can be achieved even with imprecise methods. But to understand dynamics during the phase of low numbers between plagues and to analyse the initial conditions triggering plagues may require more-precise methods. We need to determine whether two nights of trapping can provide estimates of population size and composition that are comparable to estimates obtained from 4–5 nights of trapping in agricultural landscapes. We also need to explore the use of more-attractive baits or odours to see whether we can increase trappability of individuals.

Low recapture rates may also result from nomadic movements, and we postulate that during the non-breeding period house mice become largely nomadic in agricultural landscapes. Since the non-breeding period in our area coincides with winter, it is impossible to separate these two causes of nomadism. If low food supplies are the underlying cause of nomadism, we would expect a population fed artificially in winter to remain resident, whether breeding or not. Bomford (1985) provided three types of supplemental food to a house mouse population on a rice farm in NSW during the early spring and reported a large increase in recapture rates from 24% in the control areas to 61% in the fed areas with trapping sessions 2–3 weeks apart. These results are consistent with the idea that low recapture rates and nomadic movements are a result not of cold temperatures in winter but of low-quality food supplies.

Not all feral house mouse populations have low recapture rates. DeLong (1967) studied mice in an annual grassland in California and reported 75–100% recapture rates at 2-week intervals. Stueck and Barrett (1978), working in 0·1-ha enclosures, found they could capture on average 26% of the individuals present on any given day so that population size could be estimated by enumeration. Newsome (1969) reported relatively high recapture

rates for mice inhabiting a reed bed in South Australia. Stable habitats may permit higher recapture rates because food is never as superabundant as it is in agricultural landscapes. A similar explanation for low trappability may apply to populations of the meadow jumping mouse (*Zapus hudsonius*) in North America (Boonstra and Hoyle 1986).

Newsome (1966) and Redhead (1982) rejected mark–recapture models of population estimation for feral house mice because of unequal catchability. Recent models for mark–recapture estimation overcome some of these problems of heterogeneous trap response (Pollock 1982; Jolly and Dickson 1983; Pollock *et al.* 1990). It would seem desirable to utilise these methods to gain a more precise understanding of the population dynamics of house mice with low trappability in agricultural systems.

Low trappability by itself does not invalidate standard methods of population estimation. The key question is how trappability varies with season, habitat and population density. Low trappability does reduce the precision of mark–recapture estimates (Pollock *et al.* 1990). All catch-per-unit-effort methods rely on constant catchability to achieve accurate population estimates (Caughley 1977) and we need to test this critical assumption for feral house mice before accepting the results of these methods for demographic analyses.

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