
The genus *Mus* as a model for evolutionary studies

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Dispersal in house mice

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This review evaluates direct (live-trapping) and indirect (genetic) methods to study dispersal in wild house mice (*Mus musculus*) and summarizes field and experimental data to examine the causes and consequences of dispersal. Commensal house mice (associated with human habitations, farms, food stores and other anthropogenic habitats) typically show lower rates of dispersal than feral house mice (living in crops, natural and semi-natural habitats). However, early claims of long-term fine-scale genetic structure in commensal house mice (due to low rates of dispersal) are not supported by recent data. Dispersal becomes obligatory when habitat conditions deteriorate, but most dispersal occurs below the local environmental carrying capacity and is due to social interactions with conspecifics. Excursions are relatively frequent and probably allow mice to assess the quality of habitats before dispersing. Young males have the greatest tendency to disperse, apparently prompted mainly by aggressive interactions with dominant males. If they do disperse, females integrate into new groups more easily than do males. Dispersing house mice risk loss of condition or death, but may gain reproductive opportunities on arrival in a new location. House mice can be transported passively as stowaways with humans; this contributes to population persistence and genetic structure at regional scales and has allowed house mice to spread world-wide. © 2005 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2005, 84, 565–583.

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INTRODUCTION

Dispersal is a deceptively simple concept: an individual that had been living in one location moves to another. Despite the simplicity of the concept, studies of dispersal cover many different subjects and it has been described as the ‘glue’ linking ecology, population genetics, ethology and evolution (Stenseth & Lidicker, 1992). Much has been written about dispersal of house mice (*Mus musculus*), but most data and analyses are scattered.

Dispersal in this species is of interest beyond the

obvious demographic considerations because it is an important model in evolutionary biology (Boursot *et al.*, 1993; Sage, Atchley & Capanna, 1993; Berry & Scriven, 2005, this issue), it is a pest that causes significant economic damage (Southern, 1954; Meehan, 1984; Singleton *et al.*, 2005, this issue) and it is a host for a range of zoonoses (Meehan, 1984; Singleton *et al.*, 2003). In this review, we will use data from field, enclosure, arena and laboratory studies, including genetic analysis, in order to establish the underlying causes and consequences of dispersal in house mice and to investigate the variation in dispersal according to individual characteristics and environmental and social conditions. We will also assess the impact of different spatial and temporal scales of studies.

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HOUSE MICE

Through their association with humans and their great adaptability, house mice are found throughout much of the world and can thrive in environments ranging from equatorial to sub-Antarctic (Berry, 1991). The subspecies *M. m. domesticus* is cosmopolitan, being present in western Europe, Africa, North and South America, Australasia and numerous oceanic islands. A second widespread subspecies, *M. m. musculus*, is found in eastern Europe and Asia, and a third, *M. m. castaneus*, also occurs in Asia (Boursot *et al.*, 1993). Some authors (e.g. Sage, 1981) give these forms specific status. Although this review covers *Mus musculus s.l.*, it is primarily based on research on *M. m. domesticus* in western Europe, North America and Australia. Studies of other subspecies will be specifically referred to as such.

Over much of their range house mice are predominantly commensal; that is, they are found in human dwellings, farm buildings, food stores, waste areas and other anthropogenic habitats. However, in some situations there are so-called 'feral' populations that exist away from human habitation in crops, and in natural and semi-natural habitat, usually where there are few competitors or predators. This is most notable on small islands and in Australia and New Zealand (Sage, 1981; Berry, 1991).

In high-density commensal populations (which can be up to 70 mice per m²) house mice form demes, consisting of a dominant male with females and offspring living in an exclusive territory as small as 2 m² (Selander, 1970; Gray, Jensen & Hurst, 2000). This social organization has been observed in confined populations and probably occurs in most wild commensal house mice, although field evidence is not conclusive. At the lower densities typical of feral populations (often fewer than 150 mice per ha), house mice appear less territorial, although some individuals (nursing females in particular) can become site-attached (Fitzgerald, Karl & Moller, 1981). In these situations loose groups are formed with individuals having overlapping home ranges (Triggs, 1991) or exclusive territories that are defended against members of the same sex (Berry & Jakobson, 1974; Fitzgerald *et al.*, 1981).

This variation in habitat usage and associated differences in population and social structure have a substantial impact on dispersal. A particular emphasis in this review will be the comparison of commensal and feral house mice.

DISPERSAL

Movement and dispersal influences population dynamics and also allows the movement of genes and pathogens within species. Dispersal *s.s.* is defined as a one-way movement of an individual from a home

range to a new, non-overlapping, home range (Stenseth & Lidicker, 1992). It can be divided into three stages: (1) leaving a home range or social group, (2) travelling across the landscape and (3) establishment in a new home range or group (Andreassen, Stenseth & Ims, 2002). The last stage includes the ability to breed in the new setting, which is termed 'effective dispersal'.

Some types of long-distance movement do not fulfil the standard definition of dispersal given above. Lidicker & Stenseth (1992) defined four types of 'quasi dispersal', which will also be considered in this review: (1) 'excursions' or 'exploratory movements' (temporary movements away from an established home range, with the individual returning within a short time); (2) 'migration' (seasonal movement of populations, with individuals returning at a later date); (3) 'home range shift' (an individual travels across the landscape by slowly extending its home range in one direction while constricting it in another); and (4) 'nomadism' (individuals move across the landscape without establishing a home range).

METHODS FOR STUDYING DISPERSAL

RECAPTURES OF MARKED INDIVIDUALS

The most common method for quantifying movements in house mice is capture-mark-recapture (CMR) using live traps, although other 'recapture' methods, such as footprint tubes, have been used (Fitzgerald *et al.*, 1981). Simply estimating the rate of dispersal directly from the numbers recorded moving, as many authors do, is not ideal, but despite its limitations the proportion of the population recorded 'dispersing' is commonly presented in published studies and so cannot be ignored. However, the following criticisms should be considered.

First, CMR studies in house mice are hampered by low recapture rates that vary over time, between individuals, between locations and according to capture history (Crowcroft & Jeffers, 1961; Gérard, Bauchau & Smets, 1994; Drickamer *et al.*, 1999). Consequently, CMR studies have relatively small sample sizes and even fewer observed movements. Partitioning data by breeding season or age, for example, results in low power for statistical tests.

Secondly, most CMR study areas are too small to record long-distance movements adequately, i.e. of the order of 180 m as demonstrated for house mice overnight (Stickel, 1979; Pocock *et al.*, 2003), let alone movements of more than 1.5 km, as recorded over longer time periods (Berry, 1968; Tomich, 1970; Sage, 1981; Shchipanov, 2003). Several researchers have partially overcome this problem by trapping in two grids up to 200 m apart and recording the movement

of individuals between grids (DeLong, 1967; Newsome, 1969a; Twigg, Singleton & Kay, 1991).

Thirdly, dispersal is strictly defined in relation to an individual's home range, but the relatively low numbers of recaptures in most CMR studies of house mice makes it difficult to establish the extent of home ranges (although see Berry, 1968; Fitzgerald *et al.*, 1981; Triggs, 1991). In response, authors often use surrogate definitions for dispersal: for example, movement greater than a certain distance (Rowe, Quy & Swinney, 1987), into trapping grids (DeLong, 1967), out of enclosures (Lidicker, 1976), between grids (Newsome, 1969a) and between buildings (Rowe *et al.*, 1987; Krasnov & Khokhlova, 1994). Although these measures can provide some information on movement, they are arbitrary and not readily comparable with one another (see Fig. 1). Pocock *et al.* (2003) have exploited the use of a Geographic Information System (GIS) to define subgroups (postulated to be one or more closely located demes) within a commensal population, and then defined dispersal as movement between these subgroups. This study also took account of the varying detection rates over distance, avoiding a bias that normally causes long-distance movements to be underestimated (Turchin, 1998).

An alternative way of analysing CMR data is to plot the distribution of movement distances between recaptures or between first and last capture. Although these graphs (known as 'distance decay curves') do not distinguish between movements within and between home ranges, the shape of the tail of the curve provides information about the frequency of long-distance movements (limited by the geographical extent of the study). Figure 2 shows distance decay curves produced from data in published studies on house mice. Although the frequency of sampling and geographical extent differ between these studies, some general trends can be observed: the curves show a sharp decline in the frequency of movements as distance increases; and males appear more likely than females to move long distances. A power curve, of the form $y = ax^{-\beta}$, was fitted by Pocock *et al.* (2003) to their movement data for house mice (Fig. 2A). The distance decay exponent (β) specific to this study was 1.42. The exponent would be higher in studies recording a higher proportion of longer movements (e.g. feral house mice or other small mammals), but as yet there is no similar study with which to compare this result.

Often house mice caught only once in a CMR study are viewed as 'transients' or 'nomads', i.e. individuals moving through the study site (Caldwell, 1964; Newsome, 1969b; Adamczyk & Walkowa, 1971; Singleton, 1983; Krebs, Singleton & Kenney, 1994). However, high rates of apparent transience are found in populations closed to movement, as a simulation study carried out by one of us (M. J. O. Pocock, unpubl. data)

demonstrates. In a population of 50 individuals with survival rate set at 0.6 per month and recapture rate at 0.3 per month, sampled over 10 months (typical of many house mouse studies), the average rate of apparent transience was 64%. Even when the survival rate was set at 0.9 per month and recapture rate at 0.6, the number of 'transients' was still 15% of the total number caught.

Direct data on immigration can provide a useful perspective on dispersal (e.g. Newsome, 1969b). The age/mass structure of newly caught house mice allows recruitment via immigration to be distinguished from recruitment via *in situ* reproduction (DeLong, 1967; Adamczyk & Walkowa, 1971), particularly using robust statistical methods (Nichols & Pollock, 1990). Unfortunately, the source of immigrants may not always be verifiable and may even be located in untrappable areas within a study site (Pocock, Searle & White, 2004).

Other statistical models have been used to estimate rates of dispersal (reviewed in Bennetts *et al.*, 2001), but to our knowledge, only multistate CMR models have been applied to house mice (Pocock, 2002). Multistate models estimate rates of recapture and survival, as with single-state CMR models, but also estimate rates of transition between states (e.g. movement between geographical locations). They show great potential for the analysis of dispersal studies but do require relatively large sets of high-quality data.

OTHER DIRECT FIELD METHODS

Radiotelemetry has been little used in studies of house mice because radio-transmitters with sufficiently long battery life can only be used on adult mice (Chambers, Singleton & Krebs, 2000). It is also difficult to track mice in commensal habitats due to the shielding and reflection of radio signals by bricks and metal. However, the technology has been successfully used to track commensal house mice forced to disperse from a grain crib as it was emptied (Baker & Petras, 1986) and also has been used to record changes in home range size of feral house mice over short periods of time (Krebs, Kenney & Singleton, 1995; Chambers *et al.*, 2000). Krebs *et al.* (1994) used the loss of radio-tagged individuals from a study site to provide an estimate of the number of dispersing or nomadic individuals.

LABORATORY AND ARENA STUDIES

Early studies on captive house mice simply defined dispersers as escapees from 'escape proof' pens (Myers, 1974), but the definition of a disperser has since become more sophisticated and, arguably, more contrived (see Table 1). In large arenas, where social interactions can be directly observed and territorial boundaries plotted,

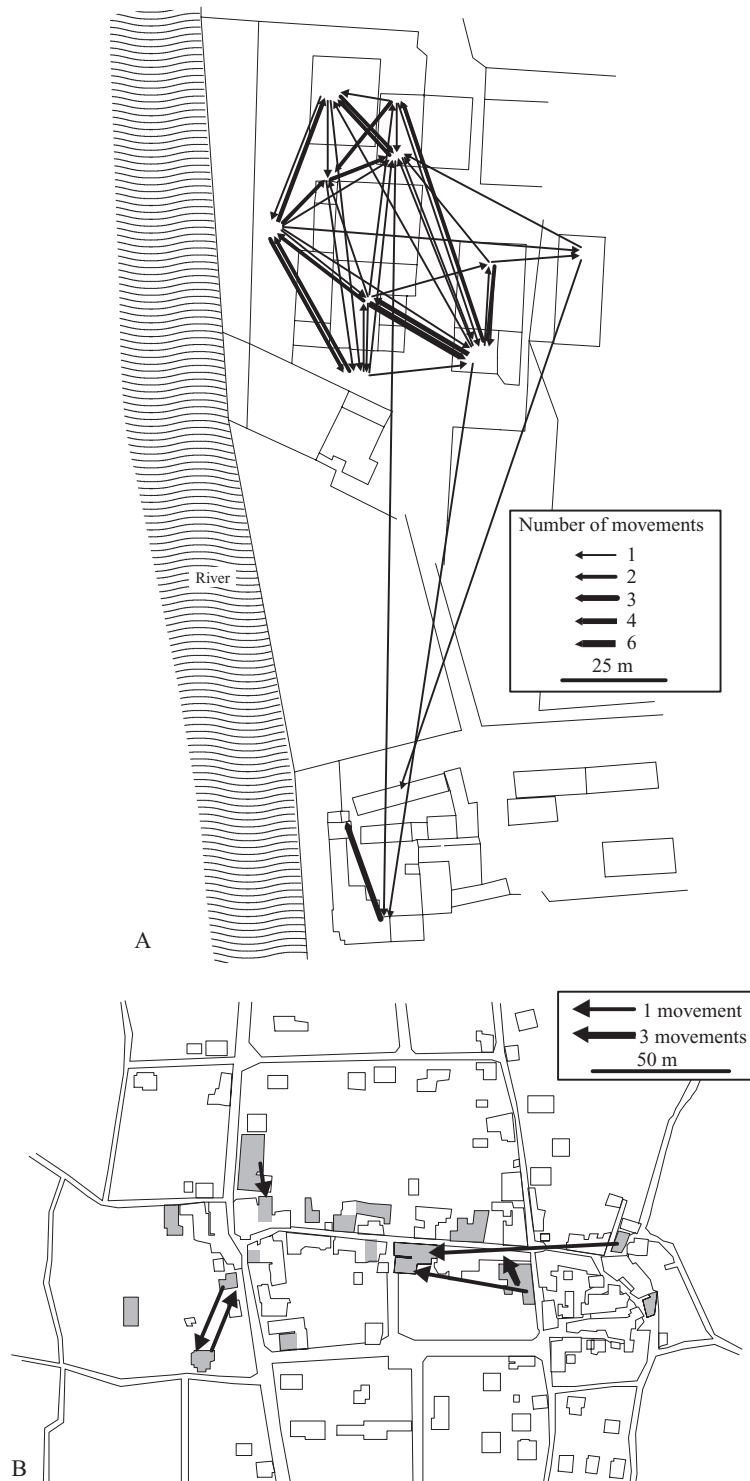


Figure 1. Dispersal in two commensal house mouse populations from capture–mark–recapture studies. The rate of dispersal depends partly on the definition of dispersal and the spatial and temporal scale of the study. A, dispersal on two farms (0.3 and 0.7 ha) separated by 80 m in Yorkshire, UK (Pocock *et al.*, 2004). The study consisted of 7-day trapping periods every month for 25 months. Dispersal was defined as movements between subgroups (Pocock *et al.*, 2003) and represented 7% of the 1053 recaptures. B, dispersal in Tovo S. Agata, Lombardy, Italy (human population 550) (H. C. Hauffe, unpubl. data). The study consisted of traps placed in the buildings shaded grey for 5-day trapping periods approximately every 10 weeks for 16 months. Dispersal was defined as movement between buildings and represented 2% of the 460 recaptures.

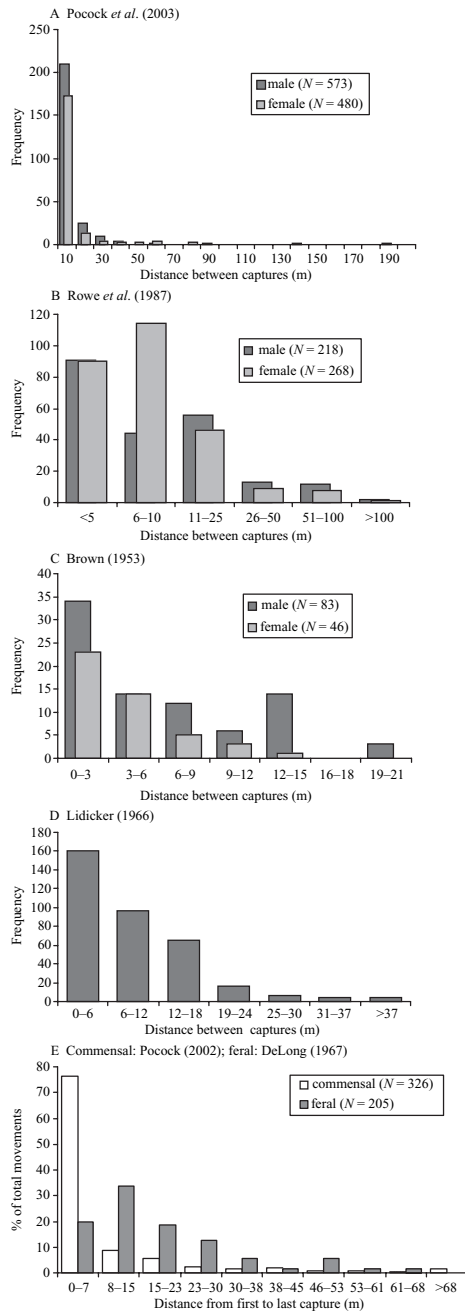


Figure 2. Distance decay curves for movements between recaptures for commensal house mice (A–C) and feral house mice (D), and distance from first to last capture for feral and commensal house mice (E). A, movements within and between buildings on two farms (0.7 and 0.3 ha) separated by 80 m, Yorkshire, UK. B, movements in a 1.5-ha site of farm buildings with nearby hedgerows, Sussex, UK. C, movements in a 720-m² hay loft on a mixed farm, Maryland, USA. D, movements in a 0.18-ha trapping grid on natural grassland, Brooks Island, California, USA. E, movements of commensal house mice in the same study as in A compared with movements of feral house mice in a 0.32-ha trapping grid in annual grassland, Virginia, USA.

dispersal can be measured at the fine scale as movement out of a deme (Crowcroft & Rowe, 1963; Reimer & Petras, 1967). Laboratory and arena studies are valuable because they can provide information on the differences between dispersers and non-dispersers (Myers, 1974), the social factors influencing dispersal (Van Zegeren, 1980; Gerlach, 1990) and the results of preventing dispersal (Van Zegeren, 1980). Rates of dispersal are typically higher in studies of captive house mice than in natural populations (Table 1), but more individuals are scarred or wounded than in natural populations (Crowcroft & Rowe, 1963; Van Zegeren, 1980). This suggests that social dynamics are altered in artificial conditions and the results should not be applied uncritically to natural populations.

GENETIC METHODS

Patterns of genetic variation have been analysed using a variety of markers in the house mouse. Early studies involved allozymes (Petras, 1967a; Selander, 1970) and *t*-alleles (Lewontin & Dunn, 1960), but microsatellites (Dallas *et al.*, 1995, 1998; Panithanarak *et al.*, 2004) and mitochondrial (mt) DNA markers (Ryan, Duke & Fairley, 1993; Jones *et al.*, 1995) are now commonly used. If populations or subpopulations differ substantially in gene frequency, this indicates a lack of dispersal over recent generations; similarities in gene frequency indicate recent common history or frequent dispersal. Although precise estimates of dispersal rates are difficult to achieve from such comparisons (Whitlock & McCauley, 1999), they do reflect the incidence of dispersal over several generations and provide evidence for effective dispersal (i.e. dispersal followed by successful breeding). Differences in effective dispersal between males and females can be distinguished using appropriate genetic markers (Y chromosomes and mtDNA, respectively), but only inconclusive results have so far been obtained for house mice (Jones *et al.*, 1995).

Genetic markers are particularly applicable to an experimental approach. Both Baker (1981) and Berry *et al.* (1991) studied the spread of introduced novel alleles into house mouse populations to estimate the extent of dispersal. Markers can also provide data at all geographical scales in contrast to CMR techniques, which can only provide information on local dispersal. Genetic markers have been used to reveal the source of colonization or recolonization events in house mice at regional and global scales (Prager *et al.*, 1993; Gündüz *et al.*, 2001).

OTHER INDIRECT METHODS

Like the genetic approach described above, the typing of pathogens provides an indirect method to

Table 1. Reported dispersal rates for commensal, feral and captive house mice (*Mus musculus domesticus*) with recorded instances of bias towards greater dispersal for a particular sex or age group

Reference	Dispersal rate (no. of dispersers out of the total)	Number of dispersers				Bias in dispersers	Definition of dispersal, location of the study site and further details of study
		Male		Female			
		Ad	Y	Ad	Y		
COMMENSAL HOUSE MICE							
Pocock <i>et al.</i> (2004)	17% (56 of 326)	38		18		Male ($P = 0.010$)	Movement between subgroups (see Pocock <i>et al.</i> , 2003) in farm buildings on two farms, Yorkshire, UK. Young male bias in dispersal with respect to movements rather than individuals.
Singleton (1983)	37% (19 of 52)	4	6	3 or 4	5 or 6	–	Between 2 adjoining cages (160 m ² each) and adjacent long grass. Aviaries near Melbourne, Australia. No movement to trapped areas of grass 15 and 150 m away.
Petras (1967a)	17% (2 of 12)	–	–	–	–	–	Movement between buildings on farms, mostly > 5 m apart, on six farmsteads, Michigan, USA.
Petrusewicz & Andrzejewski (1962)	5% (21 of 429*)	14		7		–	Movement between a loft and other parts of a building.
A. C. Frantz & D. P. Cowan (unpubl. data)	21% (319 of 1498)	148		171		No bias ($P = 0.248$)	Movement between farm buildings on one farm, Sussex, UK.
A. C. Frantz & D. P. Cowan (unpubl. data)	14% (182 of 1279)	97		85		No bias ($P = 0.366$)	Movement between farm buildings on a second farm, Sussex, UK.
Walkowa <i>et al.</i> (1989)	10% (100 of 954*)	51		49		–	Movement between pens (150 m ²) in a permeable enclosure or out of the enclosure.
Rowe <i>et al.</i> (1987)	12% (51 of 412)	34		17		Male ($P = 0.012^{**}$)	Movement between 'sites', i.e. outside a building, a separated building or a hedgerow on a farm, Sussex, UK.
Reimer & Petras (1968)	10% (6 of 59)	1	1	3	1	–	Movement from building to field, or vice versa in two farms, Ontario, Canada. No movement between buildings.
Evans (1949)	2% (4 of 256*)	0	1	1	2	–	Movement between a seed house (82 m ²) and adjacent fields, California, USA.
H. C. Hauffe (unpubl. data)	5% (8 of 149)	2	2	3	1	No bias ($P > 0.05$)	One-way movement between buildings in a village, Lombardy, Italy.

Pocock <i>et al.</i> (2004)	1% (3 of 326)	3	0	0	–	–	Movement between two farms separated by 80 m, Yorkshire, UK.
H.C. Hauffe (unpubl. data)	<1% (1 of 306)	0	0	1	0	–	One-way movement between village and isolated farm separated by 320 m of inhospitable fields, Lombardy, Italy.
Strecker (1954)	(91 of unknown)	35	12	42	2	–	Movement from a basement to snap-traps elsewhere in building, University of Wisconsin, USA. (12 of 42 adult females were pregnant.)
Rowe <i>et al.</i> (1963)	–	166	19	28	19	Male ($P = 0.001$)	Movements out of corn ricks in fields before threshing, Hampshire, UK.
Baker & Petras (1986)	10% (16 of 163*)	12	0	4	0	Male ($P = 0.018^{***}$)	Recapture in fields of house mice caught in corn cribs as they were being emptied, Ontario, Canada.
FERAL HOUSE MICE							
Stickle (1979)	26% (35 of 134)	–	–	–	–	–	Movement out of a home range (including exploratory movements and shifting home range) on two adjacent arable fields, Maryland, USA.
Lidicker (1966)	(18 individuals)	–	–	–	–	No bias	Change in home range location of individuals caught at least 5 times in 0.18 ha trapping grid on natural grassland, Brooks Island, California, USA.
Triggs (1991)	15% (25 of 162)	10	–	15	–	No bias ($P = 0.627^{***}$)	Moved home range by >10 m during winter, Isle of May, Forth of Forth, Scotland, UK.
Myers (1974)	11% (45 of 395)	30	–	15	–	Grid 1: Male ($P < 0.05$); grid 2: no bias ($P > 0.05$)	Movement >33 m within each of two 0.47 ha trapping grids on an old arable field, Grizzly Island, California, USA.
Myers (1974)	(11 individuals)	4	–	7	–	Female	Movement between two 0.47 ha trapping grids 92 m apart (as above).
Newsome (1969b)	9% (45 of 525)	29	–	16	–	Male	Movement between trapping grids (0.09–0.82 ha) in a wheatfield and an adjacent reedbed, South Australia. Maximum distance between grids was 183 m.
Berry & Jakobson (1974)	23–31%	–	–	–	–	No bias towards breeding females	Movement from one trapping grid to another on a 100 ha island, Skokholm, Wales, UK.

Table 1. *Continued*

Reference	Dispersal rate (no. of dispersers out of the total)	Number of dispersers				Bias in dispersers	Definition of dispersal, location of the study site and further details of study
		Male		Female			
		Ad	Y	Ad	Y		
Krebs <i>et al.</i> (1994)	9–28% (8–33 of 93)	7–20	1–13	1–13	No bias ($P > 0.326$)	Radiotracked individuals 'known' to have moved >100 m (lower figure) with the addition of those lost within 3 days of collaring (higher figure) in agricultural fields, Queenstown, Australia.	
Twigg <i>et al.</i> (1991)	(0 individuals)	–	–	–	–	Movement between nearby soybean fields and between fields 5 km apart, New South Wales, Australia.	
DeLong (1967)	–	4	25	6	29	–	Movement out of a 0.32 ha trapping grid in annual grassland, Virginia, USA.
LABORATORY AND ARENA STUDIES							
Lukyanov, Walkova & Adamczyk (1994)	–	–	–	–	–	Male ($P < 0.001$)	Instantaneous rate of emigration from permeable pens (600 m ²), estimated with non-linear regression models.
Lidicker (1976)	<2% (60 of 3000 +)	17	1	3	1	Adult male	Escape or emigration tendency from 'secure' enclosures. (Many individuals were not aged or sexed.)
Maly, Knuth & Barrett (1985)	44% (27 of 61)	12	–	15	–	No bias ($P > 0.20$)	Between eight 0.1 ha enclosed grids linked by gates.
Van Zegeren (1980)	16% (9 of 57)	–	–	–	–	–	Residence in an 'emigration cage' peripheral to the main colony for 3 days.
Butler (1980)	22% (36 of c. 166)	–	See right	1	See right	Subordinate ($P < 0.005$), but neither sex ($P > 0.05$)	Capture in an emigration cage accessed by swimming across a water basin. 35 'subordinate' mice moved, but sex is unknown. Summary of 20 trials in large and small enclosures.
Gerlach (1990)	55% (159 of 288)	109	–	50	–	–	Remaining in 'emigration cage' for 4 days – access to the cage was by swimming across a 60 cm water basin.

As far as possible the studies are ordered according to the spatial scale by which dispersal is defined, from the smallest to the largest scales. The dispersal rate is the number of dispersers out of the total number of individuals caught twice or more (except those marked *, where the total represents all individuals captured). Where information is available, the number of dispersers is categorized by sex and age (Ad, adult; Y, young, including both 'juvenile' and 'subadult' mice where they are distinguished). Biases in favour of particular categories of dispersers are given with the significance value provided in the study (those marked ** were calculated retrospectively by us). If a bias in dispersers was reported without statistical evidence or summary data then no significance value is given. See each quoted study for further details.

study dispersal in house mice. *Salmonella* spp. are transmitted by faecal–oral contamination in house mice and one study showed that some strains persisted in individual barns on farms and did not spread to other buildings (Henzler & Opitz, 1992). This suggests that movement of individuals and interaction with members of other groups was limited on these farms.

DISPERSAL IN COMMENSAL AND FERAL POPULATIONS

DISPERSAL IN COMMENSAL HOUSE MICE

Dispersal in stable commensal habitats occurs at lower rates and involves shorter movements than for feral house mice (Figs 1, 2; Tables 1, 2). Distance decay curves show that most recaptures are within a

Table 2. Average distance moved between captures of house mice (*Mus musculus domesticus*). Feral mice tend to move greater distances than commensal house mice, but there is considerable variation in spatial and temporal scale between studies

Reference	Average distance moved between recaptures (m)	Detail of study
COMMENSAL HOUSE MICE		
Young, Strecker & Emlen (1950)	3.7	Movement in buildings on a university campus, Wisconsin, USA.
Brown (1953)	5.2	Movement in a 720 m ² hay loft on a mixed farm, Maryland, USA.
Reimer & Petras (1968)	0.9 (in corn crib) 5.7 (in barns) 29.9 (in fields)	Movement in farm buildings and nearby fields, Ontario, Canada.
Stickel (1979)	4.0	Movement in a three-story barn, 144 m ² floor area, isolated from other buildings in fields, Maryland, USA.
Singleton (1983)	'1–2' from main nesting site	Movement within and around aviaries in a wildlife sanctuary, Melbourne, Australia.
Baker & Petras (1986)	81	Average distance moved from empty corn crib to recapture in fields, Ontario, Canada.
Pocock (2002)	3.9	Distance between recaptures on two adjacent farms, Yorkshire, UK.
FERAL HOUSE MICE		
Baker (1946)	32.7 (males) 27.2 (females)	Movement within a 1.2 ha grid of grassland, forest and plantation, Guam, Mariana Islands.
Lidicker (1966)	9.5	Movement in 0.18 ha trapping grid. Grizzly Island, California, USA.
DeLong (1967)	8.2–22.8 (male) 9.6–15.6 (female)*	Movement on plots in annual grassland, Virginia, USA. (Range indicates the difference between non-breeding and breeding season, respectively.)
Myers (1974)	7.6–10.7	Movement within two 0.47 ha trapping grids on an old arable field, Grizzly Island, California, USA.
Anderson <i>et al.</i> (1977)	41.4 (male) 43.7 (female)**	Movement in natural vegetation on a 3.1 ha island, Gull Island, Connecticut, USA.
Stickel (1979)	20.7 (male) 17.7 (female)	Movement in two adjacent arable fields, Maryland, USA.
Navajas y Navarro, Cassaing & Croset (1989)	28.6 (male) 18.9 (female)	Movement in a 3.76 ha quadrat in natural vegetation, Corsica.
Navajas y Navarro <i>et al.</i> (1989)	112 (male) 85 (female)	Movement on a 18 ha grid in a dune complex, Carmargue, France.
Twigg <i>et al.</i> (1991)	10.9	Movement in four 0.5 ha grids in different soybean fields, New South Wales, Australia.

*Values are distances from first to last capture.

** Values are the mean maximum distances moved.

few metres of previous captures (Fig. 2A–C; Singleton, 1983), and even the distance between first to last capture is small (Fig. 2E); only a very small proportion of commensal mice move more than 25 m. We can conclude that commensal house mice generally do not move far and rarely disperse. Dispersal is biased towards male mice, particularly young males (Table 1; Pocock *et al.*, 2004).

Some of the long-distance movements recorded in commensal habitats are not true one-way dispersal movements. In a study on a British farm, four of 19 individuals (21%) caught twice or more after a dispersal movement were recaptured at their original position after moving up to 50 m (Pocock, 2002). In an Italian village, H. C. Hauffe (unpubl. data) found that two out of 13 (15%) apparent dispersers returned to their original location after moving up to 90 m. Excursions of this sort have also been well documented from corn ricks [involving 14% of individuals in Rowe, Taylor & Chudley (1963) and 54% of males and 61% of females in Singleton (1985)]. Gradually shifting home ranges have not been recorded in commensal house mice, probably because there are many fixed landscape features which provide stable territorial boundaries.

The creation or destruction of commensal habitat suitable for house mice provides different conditions for dispersal. Disturbance occurs in many farms on a regular basis, particularly those with seasonal grain stores or those housing livestock at certain times of year. This may have been the cause of the dramatic movement of house mice from farm buildings into the fields in spring described by Carlsen (1993) for *M. m. musculus* in Denmark. Dispersal of this entire population occurred over a few weeks on two separate farms. Carlsen (1993) recorded the return movement from field margins to buildings in the autumn, and related this to an increase in the number of competing native small mammals in the fields. The movement of commensal house mice into fields during the summer is apparently common in temperate regions (Rowe *et al.*, 1987; Walkowa, Adamczyk & Chełkowska, 1989; Montgomery & Dowie, 1993). Some populations move outside but remain very close to buildings (Anderson *et al.*, 1977) and some do not have outdoor periods at all (Brown, 1953). The movement of house mice from indoor to outdoor habitats blurs the distinction between commensal and feral mice. In analogous fashion to feral mice, house mice in outdoor habitats near farm buildings move more frequently and further than individuals within the buildings (Brown, 1953; Reimer & Petras, 1968; Rowe *et al.*, 1987).

Rowe *et al.* (1987) investigated recolonization of commensal habitat by eliminating house mice from an isolated British farm and found that mice immigrated to the farm within 6 weeks, presumably from outdoor

habitat surrounding the farm. Similarly, field populations of house mice were the source of colonizers for British corn ricks in the mid-1900s, when such ricks were a common means of storing grain. Dispersers from the dismantled ricks supplemented the dwindling field populations, which in turn colonized new ricks constructed after harvest the following year (Southern & Laurie, 1946; Rowe *et al.*, 1963).

DISPERSAL IN FERAL HOUSE MICE

Feral house mice generally have higher rates of dispersal than commensal mice (Table 1) and their distance decay curves appear to show less rapid declines (Fig. 2D). Distance decay curves also show that the majority of feral mice move between their first and last capture, unlike commensal mice (Fig. 2E). Feral mice also tend to move greater distances between captures than commensal house mice (Table 2) and dispersal is less strongly biased towards males (Table 1).

House mice inhabiting croplands move in response to changes in the availability of suitable habitat (Singleton, 1989; Chambers, Singleton & van Wensveen, 1996). There are often permanent populations in permanent habitats such as field margins from which mice colonize standing crops (Newsome, 1969b; Singleton, 1989). Emigration from standing crops later in the season is initiated by food shortages (DeLong, 1967), harvest (Rowe *et al.*, 1963; Newsome, 1969b) or the preferable qualities of nearby fields (Stickel, 1979).

Dispersal in feral house mice also varies seasonally, independent of changing habitat quality. In temperate areas, feral house mice generally do not breed during the winter (Bronson, 1979; Singleton *et al.*, 2001). With the onset of breeding in the spring, movement distances increase (DeLong, 1967; Berry, 1968; Newsome, 1969a, b), probably due to competition between females for breeding sites and between males for access to females (Krebs *et al.*, 1995).

Excursions appear to be frequent in feral house mice (12% of individuals in Stickel, 1979) and home range shifts have also been recorded (Lidicker, 1966; Anderson *et al.*, 1977; Stickel, 1979). Nomadic mice constitute some fraction of feral populations and they occur in larger numbers in the non-breeding season, particularly in agricultural areas, where nomadism is apparently caused by poor or ephemeral food supplies and intraspecific aggression (Myers, 1974; Krebs *et al.*, 1994; Kozakiewicz & Szacki, 1995).

DISPERSAL AS STOWAWAYS

Dispersal is usually active, that is, an individual chooses to leave its home range and actively searches

for a new one, but it can also be passive, when an individual inadvertently becomes a stowaway of humans. Passive dispersal is a specialized form of long-distance dispersal, uncommon in most vertebrates. It can have major consequences on range expansion and disease transmission, but it is rarely considered in the literature (but see Cohen, 2002). Commensal house mice are predisposed to be successful stowaways because they often hide inside their food supply, do not require drinking water and can reproduce in transit. Anecdotal evidence collated by Baker (1994) shows they are frequently transported in vehicles carrying agricultural and waste products.

The extent of overseas transport is considerable, according to Baker (1994). She estimated that in the USA seven mice are transported per 100 tonnes of grain and 70 per 100 tonnes of hay or straw. Given that 550 000 tonnes of hay and straw were exported from the USA in the year of her study, this implies that tens of thousands of house mice passively leave the USA alone every year. Clearly, there is also transport of mice from other countries. Suzuki (1980) observed such stowaways on two overseas cargo boats.

THE CAUSES OF DISPERSAL

ENVIRONMENTAL CAUSES OF DISPERSAL

Populations of house mice rarely increase to the carrying capacity (K) of the local environment (the maximum number sustainable given the local conditions), presumably because social interactions limit their density. However, the carrying capacity can be exceeded, with consequences for dispersal. During plagues of feral house mice (which can be up to six mice per m^2) local densities dramatically exceed K , resulting in mass mortality (Singleton *et al.*, 2005, this issue). In such situations mice are not breeding, have no reason to be site-attached and so become nomadic in a search for food (Singleton, 1989; Krebs *et al.*, 1994, 1995). If the habitat quality or quantity is suddenly reduced, the population size will also become greater than K . Individuals then faced with a lack of food or shelter either disperse (i.e. forced dispersal) or suffer a lower survival rate through starvation or predation (Ylönen *et al.*, 2002). For both commensal and feral house mice, reduction in K is often due to human activities: for example, emptying a grain store (Baker & Petras, 1986), cleaning a barn (Pocock *et al.*, 2004) or harvesting a crop (Newsome, 1969a). Non-anthropogenic changes, such as seasonal rains (DeLong, 1967) or other 'progressively unfavourable conditions' (Lidicker, 1966) may also change K and so prompt dispersal. In these situations, mass long-distance dispersal occurs, causing population mixing (Baker & Petras, 1986).

BEHAVIOURAL CAUSES OF DISPERSAL

Dispersal in commensal populations is primarily a result of crowding (a combination of local density and complexity of the environment). It may be completely absent when populations are small, but becomes progressively more frequent as populations increase in size (Strecker, 1954; Rowe *et al.*, 1963). H. C. Hauffe (unpubl. data) studying house mice in an Italian village found that most long-distance movements occurred in the autumn when populations were growing, even though local food supplies were plentiful and survival rate was high.

When the possibility for dispersal is excluded, captive populations normally plateau in numbers, due to infanticide and hormonal interactions delaying oestrus in subdominant females (Southwick, 1955; Van Zegeren, 1980). In addition, there are high levels of wounding due to aggressive interactions, and sometimes disease (Southwick, 1955; Crowcroft & Rowe, 1963). Limited evidence from CMR studies is supported by laboratory studies that show that the majority of dispersers are young, subordinate males (Table 1), probably dispersing in response to aggressive interactions with dominant males (Gerlach, 1990). However, females also disperse (Table 1) and after dispersal they become reproductively active within a few days (Crowcroft & Rowe, 1957; Myers, 1974; Lidicker, 1976; Baker & Petras, 1986). Although females generally disperse less frequently than males, they integrate more readily into new social groups (Reimer & Petras, 1967; Lidicker, 1976) with virgin females accepted most readily (Parmigiani, Palanza & Brain, 1989, but see References therein). Competition between females for suitable nest-sites is a cause of dispersal in lower density feral populations in addition to aggressive interactions by adults towards young (Krebs *et al.*, 1995).

Interspecific, as well as intraspecific, interactions can promote dispersal. Lidicker (1966) found increased movement of feral house mice after the introduction of voles into an island population, and Carlsen (1993) related the migration of *M. m. musculus* from fields to increasing populations of other small mammal populations. Whether interspecific competition is direct (via social interactions) or indirect (via resource depletion) is not known.

VACUUM EFFECTS AND EXPLORATORY MOVEMENTS

Behavioural and environmental causes of dispersal are largely 'pushes' that instigate emigration but occasionally house mice move to a new area simply because it is more suitable. Animals appear to be 'pulled' to such places, so this may be called a 'vacuum effect'.

House mouse populations can rapidly expand to fill empty suitable habitat in the vicinity of occupied habitat (Adamczyk & Walkowa, 1971; Fitzgerald *et al.*, 1981). Presumably individuals perceive the lack of neighbours and/or territorial aggression and move to the new area. Dispersal of this type arises when habitat becomes available for recolonization, such as for commensal mice after pest control operations on farms (Rowe *et al.*, 1987). Regarding feral mice, Stickle (1979) reported the mass movement of 41 individuals from one field to a neighbouring one as ground cover increased in the second field. It is presumably through excursions that house mice detect the new suitability of nearby areas because they are most frequent when local knowledge is particularly valuable, i.e. before they first establish a home range and when in poor-quality habitat (Anderson *et al.*, 1977; Tattersall, Smith & Nowell, 1997).

THE PROCESS OF DISPERSAL

Although the causes and consequences of dispersal in house mice are relatively well known, the process of dispersal is less well understood. Leaving a home range appears to be an abrupt shift in behaviour, not associated with increased movement within a home range (DeLong, 1967) but the specific cues that trigger it are not known. Subsequent movement across an unfamiliar area could potentially be swift and direct. One mouse experimentally displaced by 250 m moved at an average speed of 80 m h⁻¹ to return to its point of capture (Anderson *et al.*, 1977). Owing to the difficulties associated with CMR and radiotelemetry, few studies have directly traced natural movements of house mice; however, when dispersing in outdoor habitats house mice probably prefer to follow landscape features, such as field margins (Berry, 1968; Carlsen, 1993). The risks associated with dispersal movements in house mice, such as increased predation and failure to find food, have not been quantified, but must be considerable.

Immigration, the final stage of dispersal, is easiest into suitable habitat that contains no mice (Crowcroft & Rowe, 1963), but nevertheless colonization of empty habitat is often unsuccessful (Anderson, 1964; Lidicker, 1966; Petras & Topping, 1981; Berry, Cuthbert & Peters, 1982; Tattersall *et al.*, 1997). Results from arena studies showed that individuals introduced into pre-existing populations often died due to wounding (Lidicker, 1976; Reimer & Petras, 1967) and those that survived only did so on the margins of the arena (Van Zegeren, 1980) or at the bottom of the social hierarchy (Andrzejewski, Petruszewicz & Walkowa, 1963).

From an evolutionary perspective, one vital issue is the extent to which house mice can breed successfully following dispersal (the effective dispersal rate). The

colonization of islands by house mice clearly demonstrates that house mice have been able to breed in empty habitat to which they have dispersed and effective immigration to pre-existing populations is shown by genetic studies of hybrid zones between subspecies or chromosomal races. In such hybrid zones there is often a gradation between the two parental forms, with intermediate populations having intermediate genetic characteristics (e.g. Hunt & Selander, 1973; Searle, Navarro & Ganem, 1993). This is best explained by dispersal followed by interbreeding.

EFFECTS OF DISPERSAL

INDIVIDUAL FITNESS AND SURVIVAL

Dispersal simultaneously affects the individual, the population and the species. From the individual's perspective, dispersal in response to catastrophic disturbance of a habitat is presumably vital in ensuring its survival, because K is effectively reduced to zero (e.g. Baker & Petras, 1986). However, in other cases, dispersal is a risky process, especially for males that appear to have a lower survivorship than females, with adult males faring worse than young males (Singleton, 1983; Rowe *et al.*, 1987).

Males need to balance the costs of dispersal (such as the high risk of being predated when moving across an unfamiliar landscape, and the low probability of joining or establishing a new group), with the costs of not dispersing (such as the probability of delayed reproduction and aggressive interactions with dominant individuals) (Ylönen *et al.*, 2002). Similarly, females must balance the benefits of staying (such as communal nesting with kin, which increases reproductive success: Parmigiani, 1986) with those of dispersing (such as reactivation of oestrus).

POPULATION STRUCTURE

Even low rates of dispersal may have important effects on population dynamics (Krebs, 2003). In some cases immigration is a more important source of population growth than *in situ* reproduction (Newsome, 1969b; Myers, 1974) and it can allow populations to persist in otherwise unsuitable habitats. Such habitats can be population sinks for the least fit individuals (Newsome, 1969a; Anderson *et al.*, 1977; Chambers *et al.*, 1996; Ylönen *et al.*, 2002), but sinks are important. Commensal house mice can persist temporarily in suboptimal sink habitats when donor habitat is destroyed and later infest newly available habitat (Reimer & Petras, 1968; Baker & Petras, 1986; Rowe *et al.*, 1987) and in such circumstances house mice can reintroduce disease to previously infected livestock (Henzler & Opitz, 1992). In Australia, permanent source populations of feral mice are found in

habitat such as field margins, semi-natural habitat or farm buildings. Cereal crops are initially sinks, but become induced donor habitats as the growing season progresses, until the crop is harvested (Singleton, 1989; Kaufman & Kaufman, 1990; Chambers *et al.*, 2000).

GENETIC STRUCTURE WITHIN POPULATIONS

The earliest studies based on *t*-alleles and allozyme variation (reviewed by Berry & Jakobson, 1974; Sage, 1981) suggested that house mouse populations were highly structured. Mice in different corn ricks or neighbouring buildings on farms were found to differ considerably in frequency and types of *t*-alleles, arguing against free movement between ricks or between buildings (Anderson, 1964; Petras, 1967b). Similarly, Selander (1970) found significant differences in allele frequencies in allozymes between different parts of the same barn and Petras (1967a) reported heterozygous deficits in pooled data. In addition, when *t*-alleles were introduced into a population on Great Gull Island in New York State, they spread very slowly despite being favoured by meiotic drive (Anderson, Dunn & Beasley, 1964). These data and results from mathematical modelling (Lewontin & Dunn, 1960) appeared to show that house mouse populations are subdivided into small breeding units, with very little effective dispersal between them. The breeding units inferred in these genetic studies were explicitly equated with the demes observed during behavioural studies conducted in arenas and enclosures at a similar time (e.g. Crowcroft & Rowe, 1963; Reimer & Petras, 1967).

However, the inference from the early genetic data that effective dispersal is extremely limited in the house mouse has been called into question for several reasons. Most obviously, the inference does not reflect what we now know about dispersal in feral house mice. Indeed, Berry & Jakobson (1974) compared ecological and genetic data on an island population (Skokholm, Wales), and found the dispersion of rare allozyme alleles to be consistent with CMR data that showed substantial movement of individuals around the island. Other genetic data on feral mice indicate substantial rates of effective dispersal (Myers, 1974; Singleton & Redhead, 1990; Berry *et al.*, 1991).

CMR studies of commensal mice show lower dispersal rates and distances than for feral mice (Tables 1, 2). However, population structure for commensal mice, as revealed for example by the distribution of allozyme alleles (Selander, 1970) or by the incidence of *Salmonella* (Henzler & Opitz, 1992), is likely to be only a short-term effect. Ecological studies suggest high turnover (about six generations per year) and great flux in the spatial distribution of commensal

house mouse populations over a period of years (Pocock *et al.*, 2004; see also Baker, 1981; Singleton & Hay, 1983; Singleton, 1983). This will lead to substantial effective dispersal over such time scales and is reflected in estimates of long-term effective population size of house mouse populations in the range of 500–50 000 (Potts & Wakeland, 1990; Dallas *et al.*, 1995). Indeed, there are experimental genetic data that confirm substantial effective dispersal within a commensal house mouse population. Baker (1981) introduced a haemoglobin allele (*Hbb*^b) into a farm population where the allele was absent. She found that the introduced allele spread widely after a few generations.

Furthermore, the interpretation of *t*-allele variation has undergone a recent revision (Durand *et al.*, 1997; Ardlie & Silver, 1998) from which there is no longer an inference of highly structured house mouse populations. Consistent with this, Dallas *et al.* (1998) did not find heterozygote deficits (i.e. population structure) in a commensal population studied with microsatellite markers.

REGIONAL GENETIC STRUCTURE

Although the extent of genetic subdivision within populations of house mice has been contentious, the evidence for such structure at a regional level is unequivocal. For example, Berry & Peters (1977) demonstrated that neighbouring islands in the Faroe archipelago have radically different allele frequencies at the *Hbb* locus, with fixation or near-fixation of different alleles on different islands. Similarly, Hauffe & Searle (1993) showed that neighbouring villages in Valtellina (northern Italy) are often characterized by different chromosome races, such that five different races are distributed in a patchy fashion among 19 villages and hamlets along a 20-km stretch of river valley (Fig. 3). Also, Dallas *et al.* (1998) compared allele frequency at eight microsatellite loci among seven villages in Belgium separated by distances of 0.5–59 km and found there was substantial genetic differentiation between them.

These results indicate that there is insufficient effective dispersal of house mice at a regional level to homogenize gene frequency. Instead, at a regional level, suitable mouse habitat is found in patches (e.g. oceanic islands, villages or farms) in an inhospitable matrix and only rarely do movements between patches occur and result in successful reproduction. Some mouse populations, e.g. those on oceanic and offshore islands, are initiated by passive dispersal and are distinct at the time of formation, due to the founder effect (Berry, 1996). The founder effect (in which a small number of individuals initiating a population have only a subset of the variation present in the source population) also influences non-genetic

characters, e.g. the small number of parasitic helminths in Australian house mice (Singleton & Redhead, 1990).

Occasionally, the genetic characteristics of the mice within habitat patches may change through extinction–recolonization events. Although recolonization from a nearby population could occur by active or passive dispersal, passive dispersal from a distant population is also possible. The pattern of distribution of chromosome races in Valtellina, northern Italy (Fig. 3), illustrates this well. The Lower Valtellina (LV) and Poschiavo (POS) races appear to have spread into Valtellina from neighbouring areas whereas the Mid Valtellina (MV) and Upper Valtellina (UV) races have arisen following hybridization of the LV and POS races (Hauffe & Searle, 1993; Hauffe & Piálek, 1997; Hauffe *et al.*, 2004; Piálek, Hauffe & Searle, 2005, this issue). The UV race occurs in two separate groups of villages whereas the MV race is found centrally in adjacent villages (Fig. 3). The above authors suggested that the spread of these hybrid forms was from

particular points of origin to adjacent villages following extinction–recolonization events. The All Acrocentric (AA) race found in neighbouring villages in the south-central parts of Upper Valtellina (Fig. 3) is genetically and morphologically unrelated to the other races in Upper Valtellina (Hauffe, Fraguédakis-Tsolis & Searle, 2002) and is thought to have arrived in the valley following long-distance passive dispersal. The AA race is found in the area devastated by flooding in 1807. The local mice may have become extinct and the villages subsequently recolonized from a distant source (Hauffe & Searle, 1993; Hauffe *et al.*, 2004). Hybrids in the Upper Valtellina region are found quite frequently, reflecting effective dispersal of different chromosome races from nearby villages (Fig. 3).

Other evidence that there may be effective dispersal between local populations comes from the demonstration of isolation by distance over a scale of tens of kilometres by Ryan *et al.* (1993) and Dallas *et al.* (1995) in mtDNA and microsatellite studies, respectively.

RANGE EXPANSION

One of the most striking consequences of dispersal is the attainment of a large species range from a small area of origin. *Mus musculus* has spread from south-central Asia to being widespread in every continent (except Antarctica) and on many oceanic islands. It is believed that house mice colonized the Middle East naturally. *M. m. domesticus* was then moved around the Mediterranean basin by Bronze Age traders c. 3000 years ago (Cucchi, Vigne & Auffray, 2005, this issue) and spread much further when explorers and traders unwittingly took the subspecies as stowaways to North and South America, Africa, Australasia and many oceanic islands from the 15th century onwards (Boursot *et al.*, 1993). *M. m. musculus* and *M. m. castaneus* are commensal over much of their range and have also been transported extensively by humans, including to oceanic islands (Boursot *et al.*, 1993).

Genetic markers have revealed some of the dispersal events that allowed *M. m. domesticus* to attain its current range. For example, the 15 mtDNA haplotypes found on Madeira are very closely related to each other, suggesting a single colonization source, and the frequencies are most similar to north-west continental Europe (Table 3). One possible explanation for this is that the Vikings were responsible for transporting house mice to Madeira (Gündüz *et al.*, 2001).

CONCLUSION

Studies of farm populations of house mice indicate that many individuals rarely move beyond their place of birth. By contrast, some mice move enormous distances, courtesy of passive human transport. These

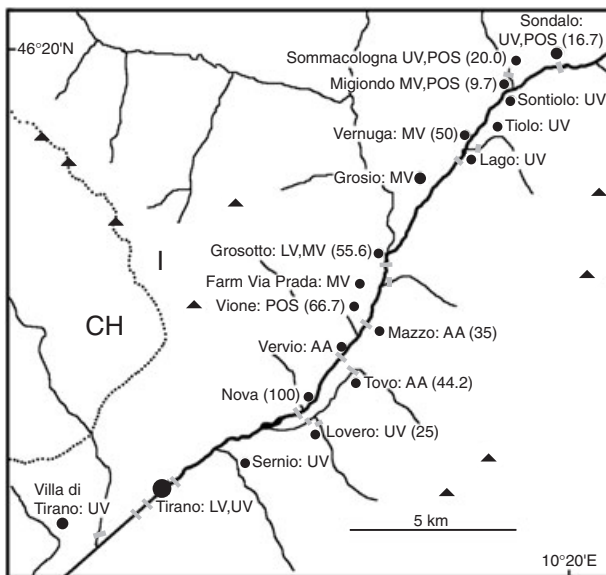


Figure 3. The villages in Upper Valtellina, northern Italy, and the chromosome races of house mice that characterize them, as follows: UV, Upper Valtellina; MV, Mid Valtellina; LV, Lower Valtellina; POS, Poschiavo; AA, All Acrocentric (see Hauffe & Searle, 1993, for a description of the races). Each village is dominated by 0–2 of these races; interracial hybrids are also present at a percentage indicated in parentheses (based on overall data for this area as presented in Hauffe *et al.*, 2004). Size of village is indicated with larger and smaller black dots. Major rivers (solid black lines) and human river crossings (grey bars) are shown as are mountain peaks greater than 2000 m above sea level (triangles) and the border between Italy (I) and Switzerland (CH) (dotted line).

Table 3. Incidence of mitochondrial D-loop haplotypes (933 base pairs) in house mice among localities on the island of Madeira, and the occurrence of these haplotypes in north-west continental Europe (northern and central Germany and Scandinavia) and elsewhere in western Europe and the Mediterranean basin

Madeiran haplotype	No. of localities where haplotype is found		
	In Madeira	In NW continental Europe	Elsewhere in W Europe and Mediterranean basin
1	8	14	
2	3	5	1
3	1		
4	1		
5	1		
6	1		
7	1		
8	2		
9	1		
10	1	1	
11	1		
12	1		
13	1		
14	2	3	
15	1	1	1
Non-Madeiran haplotypes	0	19	81

Data are taken from Prager *et al.* (1993), Nachman *et al.* (1994), Prager, Tichy & Sage (1996), Prager, Orrego & Sage (1998) and Gündüz *et al.* (2001). This dataset incorporates a total of 34 mice from 19 localities on the island of Madeira, 177 mice from 37 localities in north-west continental Europe and 190 mice from 83 localities elsewhere in western Europe and the Mediterranean basin.

two extremes are certainly extraordinary, but there is also considerable variation in dispersal patterns, according to whether the mice are commensal or feral, whether they are male or female, and many other factors.

Although this review shows that we comprehend many of the causes, processes and consequences of dispersal in house mice, there is still much to be discovered. In order fully to understand dispersal in this species, we must re-examine preconceptions, integrate the results of ecological and genetic field studies and employ more sophisticated techniques to define dispersal (e.g. the GIS approach of Pocock *et al.*, 2003).

The definition of dispersal from CMR studies is especially important for future researchers. Given the variation and flexibility of house mouse lifestyles, we

recommend that future researchers explicitly consider the spatio-temporal scale of their study and thereby define dispersal in relation to the particular characteristics of their house mouse population, and especially with respect to home range size. Further experimental field studies (such as Baker & Petras, 1986) would be valuable to indicate the causes of dispersal and the responses of individuals and populations, especially where they are controlled and replicated, although this would be a major logistical challenge. Incorporating CMR and genetic studies within the same field site will also provide additional understanding of house mouse dispersal.

In addition, we have identified that future research is specifically welcome in the following areas: (1) the specific cues that cause a resident to become a disperser; (2) the dispersal of very young mice; (3) the travelling phase of dispersal, particularly the role of landscape features; (4) the rate and role of excursions; and (5) the applicability of laboratory studies of behaviour to wild house mouse populations.

Dispersal is a rapidly maturing field of study. Given the wealth of behavioural, ecological and genetic studies already conducted on the house mouse, this species is an ideal model organism with which to develop the field.

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