Chapter 4

Wild Mice

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I. INTRODUCTION

The tractability and small size of the house mouse has made it the favorite study animal of laboratory research. The utility of the mouse for such studies was greatly enhanced by the development of highly inbred strains. Availability of these lines allowed researchers, when testing a hypothesis, to emphasize the effects of experimental procedures over possibly heterogeneous genetic backgrounds. Almost incidentally, many heritable traits were found fixed for different alleles among the strains, and this added greatly to the value of the mouse for transmission genetics studies of morphological, behavioral, and biochemical traits. The purpose of this chapter is to introduce the laboratory researcher to the biology of the nondomesticated ancestors and relatives of the laboratory mouse: the natural history and genetic variability of wild mouse populations. In addition, I will mention briefly the methodologies for field study, care, and breeding of these wild mice.

The book by Keeler (1931) should be read for the fascinating history of the earliest interactions between man and mouse—as they both became domesticated. Ten years ago Berry (1970) summarized our knowledge of wild mouse biology. This chapters expands upon that foundation, covering a decade of active research that has produced major new discoveries and caused revision of old ideas about the ecology and evolution of these animals. Bronson (1979a) presents a comprehensive review of house mouse ecology.

The taxonomy of the house mouse and the distribution of the various species was presented in Chapter 2 of this volume. From that discussion, the work by Sage and Marshall, (in prep.; Fig. 1), it is clear that a considerable amount of divergent evolution has occurred among the mice. It is also apparent that the systematic treatment has been greatly modified from the earlier view of a single widespread polytypic species (Schwarz and Schwarz, 1943). It must be understood and recognized that there are many different species hidden under the common name "house mouse." A final systematic treatment of this group is not yet possible, and as more information is obtained on native populations of house mice some subspecies populations may become recognized as different biological species. Throughout the chapter, I will stress the taxonomic identity of the populations studied in order to emphasize that much of the variation present in this complex is sometimes partitioned among genetically distinctive units.

Bruell (1970) provided a useful descriptive vocabulary for house mouse populations that will be used throughout this chapter. *Wild* mice are distinguished from *domesticated* mice. The latter are the strains that have been raised in captivity for many generations; their breeding is controlled by man. Wild mice are stocks whose reproduction is not controlled by humans. Among the wild mice are three additional groups distinguished by their degree of association with man. *Aboriginal* mice live predominantly independent of human dwellings. *Commensal* forms live in close association with man-made structures, and *feral* mice have secondarily returned to an aboriginal mode of existence from the commensal stage. The aboriginal species discussed here include *Mus abbotti*, *M. hortulanus*, and *M. spretus*. All introduced populations of *M. domesticus* in the New World and in Australia, which live in native vegetation, are considered feral forms derived from commensal ancestors.

An important point to remember from Chapter 2 is that the mice, which occupied the New World, Australia, and South Temperate oceanic islands and provided the bulk of the genome of most laboratory strains, are descendants of the western European house mouse, *M. domesticus* not *M. musculus*. Thus much of the study of wild populations has been done in areas where this house mouse is an introduced species. Consequently, many field studies have been done where the mice are nonnative and may not have had sufficient period of time to interact and achieve a stable ecological balance with the native fauna. Whether or not the ecological and physiological responses of these introduced animals are distinctive from the patterns seen in native habitats should be considered. Most of our knowledge about the range of genetic variability in this complex comes primarily from one species, *M. domesticus*. From the little information available on the biology of other house mouse species, it is certain that much greater amounts of genetic variation are present in this group than has been reported to date. Field studies of native populations of these mice from other parts of its range beyond western Europe promise to yield many interesting findings to future researchers.

The proper identification of the animals under study can sometimes be of importance, e.g., in cases of mice identified as vectors of diseases or for any comparative evolutionary study of host proviral genomes or traits of the mouse genome itself. I have pointed out possible literature mistakes like this in the text. The creation of most inbred strains of mice from hybridization of what are considered here as *M. domesticus* and *M. molossinus* creates an awkward nomenclatorial problem. Because most of the biochemically detectable proteins of inbred strains are characteristic of *M. domesticus* populations I have used that name to identify the most common laboratory strains. Whatever the solution may be to this dilemma, it is clear that animals referred to here as *M. musculus* (*sensu strictu*) played almost no role in producing the genomes of domesticated laboratory mice.

II. NATURAL HISTORY

A. General Distribution

Species in the house mouse complex have a native distribution that extends across Europe, North Africa, and the northern

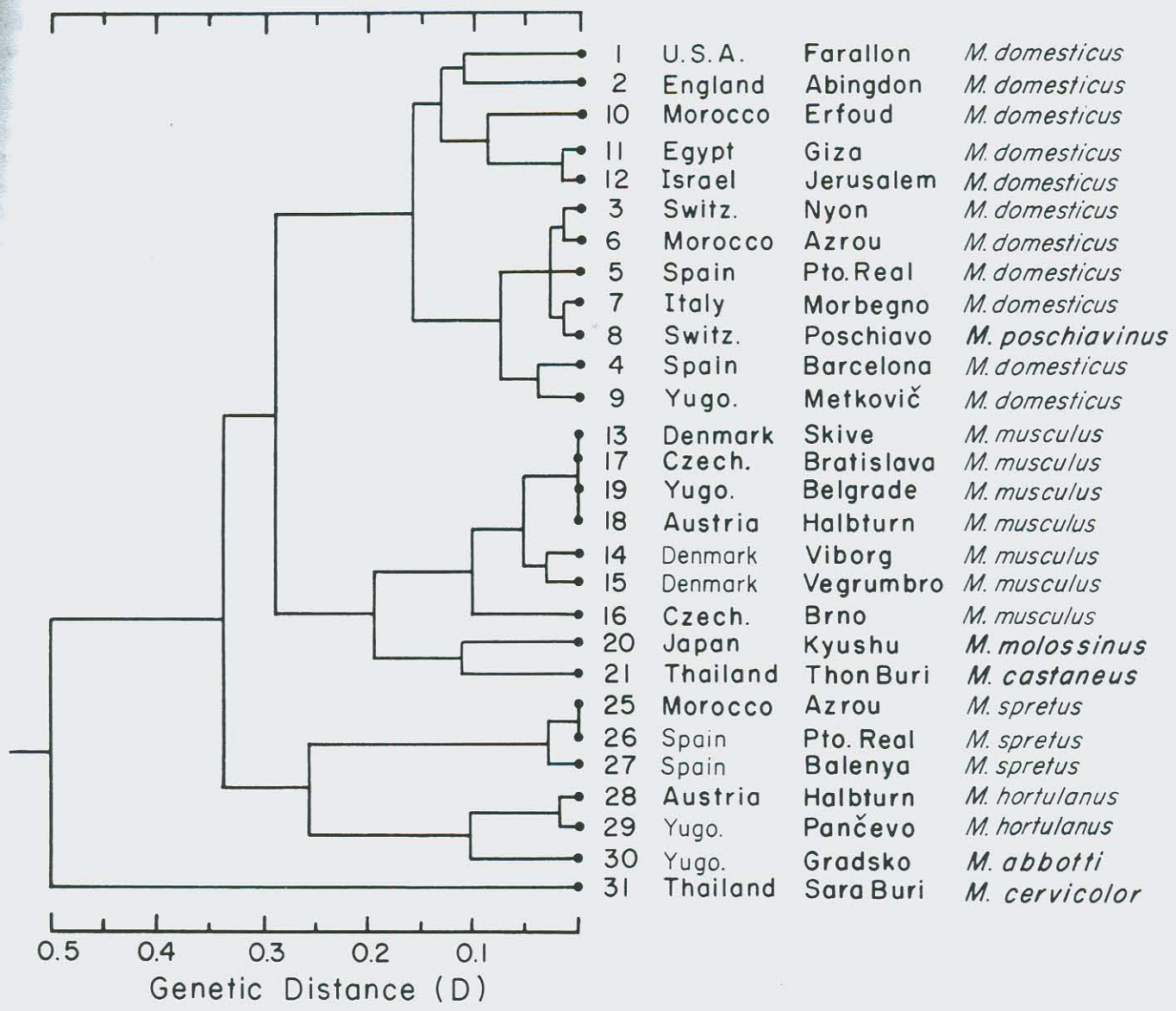


Fig. 1. Genetic relationships of single house mice assayed for 56 enzyme and protein loci using starch gel electrophoresis. Details will be presented in Sage and Marshall (in prep.).

half of Asia. The commensal species, *M. domesticus* and *M. castaneus,* have followed man into the New World, Australasia, and southeastern Africa, leaving few regions of the globe without house mice. The totality of area and the range of habitats occupied by these mice is impressive, but the distribution of each individual species is limited and may be related to historical processes of general biogeographic importance.

Our knowledge of the ranges of some taxa is not very precise. This is particularly true of the Asian species. The distributions of the three aboriginal species of Europe and Asia Minor are better understood. They conform well with the patterns shown by better studied mammalian groups, and it is reasonable to assume that similar series of biogeographical events have determined all three of these patterns. The most striking distribution is shown by the mound-building species, *M. hortulanus*. It is restricted to the steppe grassland regions of the Carpathian basin and the Ukraine (Festetics, 1961; Petrov, 1979). *Mus spretus* occurs in the warmer and mesic parts of the western Mediterranean regions, from France to Libya. A distinctive "Lusitanian" fauna occurs in this same area that is considered to be one of the oldest assemblages in the European region (Scharff, 1899). The distributional limits of *M. abbotti* is not well-known, but appears to include southeastern Europe and Asia Minor. This is a common distributional pattern reported for other groups of mammals (Atallah, 1978; Tchernov, 1975).

The ranges of these three aboriginal species coincide with patterns seen in other animal and plant groups; this suggests that they are parts of biotic assemblages, which have been shaped by large-scale environmental forces over long periods of time. Distributional limits in these species are presumably determined by specific features of geography, climate, and/or vegetation, rather than by human activities and culture.

Commensal species have in part tied their evolutionary future to the activities of man. Consequently their distributions may be determined differently than in the aboriginal forms. The occupation of so much new range by *M. domesticus* is partly a result of its tolerance for close association with human habitats such as sailing ships. In using human-assisted transportation, the founding populations of this species have been able to colonize lands and environments differing greatly in quality from their native homelands in the port cities of western Europe. As long as these animals remain commensal with man their physical environments remain similar to their ancestral ones. But as they go feral in places as disparate as moist Hawaiian forests, Australian deserts, or sub-Antarctic islands, the physical and biotic features of the habitat become increasingly dissimiler to those they left in western Europe. The factors presently controlling such introduced populations may be completely different from those produced under the influence of selection pressures in the native range. The question of the evolutionary stability of communities containing feral mice should be kept in mind. This admonition is worth making because the very large bulk of information available for wild *M. domesticus* comes from populations living in nonnative environments. Field studies are almost completely lacking of this important species in the original habitats, where selection pressures produced animals so remarkably successful in coexisting and thriving with human culture.

While the efforts of Schwarz and Schwarz (1943) to present a comprehensive taxonomy of the house mouse complex are now known to be erroneous, they did raise some provocative ideas about the origins of commensal mice. They proposed that commensal forms arose independently from three different lineages of aboriginal mice in areas where the first agricultural communities developed. Phylogenetic data based on protein similarity (Fig. 1) shows that interpretation is incorrect. All of the commensal stocks are more closely related to one another than they are to one of the putative aboriginal ancestors, *M. hortulanus*. The origin(s) and subsequent evolution of the commensal mice remains an interesting question. Further data is needed on the commensal and wild stocks of central and eastern Asia before it will be possible to distinguish between the model of a single versus multiple origin of commensal mice. The great amount of biochemical difference between the *domesticus* and the *musculus–castaneus–molossinus* lineages suggests the separation of these stocks predates the origins of human agricultural societies and supports the hypothesis of repeated origins of commensalism in house mice (Sage and Marshall, in prep.). Photographs of species of this complex are shown in Chapter 2, Fig. 4.

Fossil remains of *M. domesticus,* from the Achuelan period, approximately 80,000 years before present (BP) in Israel, provide direct evidence for the continuous presence by this form from before the development of agricultural societies until the present (Tchernov, 1968). Hesse (1979) describes the occurrence of *M. domesticus* in Iran in a preagricultural, Neolithic site. Although the relative abundance of mouse remains increased after the site became occupied by humans on a year-round basis, mice apparently lived there while the area was still a temporary human dwelling place. These data suggest that the commensal adaptation of this species was a fortuitous preadaptation of these animals to another more permanent feature of their environment, i.e., rock crevices. The ease with which this species reverts to a successful feral existence suggests that commensalism has not required much sacrifice in terms of genetic modifications of behavior, morphology, etc.

B. Microhabitat Distribution

Within the native range of the house mice their local distribution in various habitats is broad, but there are limitations. In different parts of their ranges, the species are variably constrained to particular habitats. This section reviews the types of environments where mice are found, and it is based in large part on the anecdotal information published in general faunal studies and from personal observations.

Mus hortulanus has been the most thoroughly studied aboriginal species (Naumov, 1940; Hamar, 1960; Festetics, 1961; Mikes, 1971). Throughout its range, these mice live in grain fields and remaining patches of native steppe grasslands. This species occurs in the disturbed vegetation surrounding agricultural lands and may be found in open habitats along river courses. It has not been reported in buildings, but this may be an artifact resulting from nonrecognition by taxonomists of the distinctiveness between this form and the sympatric and commensal *M. musculus*. In western Europe and North Africa, *M. spretus* has been reported from a variety of habitats (Cabrera, 1914; Lay, 1967, Fayard and Erome, 1977; R. Sage, observations). In France, it occurs in biotopes, which include a herb stratum. In Spain, it is widespread in the countryside below 1000 m elevation, in both chaparral vegetation and agricultural fields. I found them absent from second-growth woodlands adjacent to cornfields, where they were extremely abundant. In North Africa, they occur in grasslands and chaparral vegetation. While they do not appear frequently inside of buildings, I did find a case in southern Spain, which demonstrates the willingness of this species to enter this habitat. A newly constructed (three-years-old) cement-block

building in open wastelands outside of a rural town had *M. spretus* living on both the first and second floors. This was the dominant species at the time, with *M. domesticus* present in low numbers. Little information is available on the local distribution of *M. abbotti* (Kochija, 1960; Osborn, 1965; R. Sage, observations). South of the Caucasus mountains of Georgia, U.S.S.R., they live in most natural and agricultural habitats. In Turkey, they are reported in grain fields and roadside vegetation (bamboo grove). I fund them in the grassy borders of cornfields in southern Yugoslavia.

The second major lineage of house mice includes forms considered more commensal in behavior than the three just discussed. However, it is misleading to consider them obligate commensals of man, as they sometimes live in wild habitats. *Mus molossinus* has been studied in Japan and Korea (Hamajima, 1962a; Jones and Johnson, 1965). In Japan, it is found primarily in synanthropic environments: urban houses, farm buildings, farm gardens, and cultivated fields. In smaller numbers, it lives along river levees, and seasonally in pine plantations and rice paddies. In Korea, it was reported primarily in abandoned agricultural lands and along water courses. *Mus castaneus* is found only indoors in the Phillipine islands (Anonymous, 1973), Indonesia (Hadi *et al.*, 1976), Malaya (Harrison, 1955), Nepal and Thailand (Marshall, 1977), and India (Srivastra and Wattal, 1973). This may be the most obligately commensal species of house mouse. Within its range across central Asia and into northern and eastern Europe, *M. musculus* occupies a variety of habitats. At the northeastern limits of its range in Siberia, it is found primarily inside of buildings (Tupikova, 1947; Romanova, 1970). In central Russia this species does not overwinter in the natural vegetation, but retreats to synanthropic habitats such as haystacks and buildings (Shchepotiev and Levickij, 1974). In central Europe (Czechoslovakia and Poland), this species is found in buildings and in agricultural lands (Pelikan, 1974; Zejda, 1975; Dynowski, 1963). The field populations here do not persist throughout the winter, and some animals actually migrate back into buildings and stacks of hay. In a comprehensive survey, Zejda (1975) never found this species in native woodland vegetation in Czechoslovakia. To the northwest, in Denmark, they are commensal, live in agricultural fields, in meadows, and scrublands, but rarely occur in woodlands (Ursin, 1952). In the autumn, there seems to be an immigration of the field-dwelling mice into buildings, but it is not known whether some segment of this population overwinters in the fields. Further north in Sweden, this species does occur in natural habitats throughout the year, as well as in dwellings (Zimmermann, 1949). They were reported living in rocky outcrops along the northern Arctic coast, 50 km from the nearest human settlement.

As presently understood, the native distribution of *M. domesticus* and its close relatives extends from Nepal westward to North Africa and western Europe. In much of the rest of the world, it is an adventive species. In Napal, *M. d. homorus* lives indoors and in agricultural fields at elevations higher than Kathmandu, where *M. c. castaneus* is present (Marshall, 1977). It does not enter the forest habitat. Gaisler (1975), Hassinger (1973), and Roberts (1977) report that *M. d. bactrianus* is widespread in both agricultural and native habitats throughout most of Afghanistan and Pakistan at elevations below 3000 m. In Pakistan, they were found living in a barren, stony ravine far from a human settlement. The subspecies *M. d. gentilulus* lives both as a commensal and a wild species along the coastal regions of the south Arabian peninsula (Harrison, 1972). Wild populations were found living in the burrow systems of sand rats (*Meriones crassus*) in the desert. Across its range in the Middle East and North Africa, *M. d. praetextus* is widespread in buildings, in agricultural lands, and in the moister native habitats (Harrison, 1972; Atallah, 1978; Ranck, 1968; personal observations). In the circum-Mediterranean regions of Europe, *M. d. brevirostris* is found most frequently in commensal situations rather than native habitats. In southern Yugoslavia, where *M. abbotti* lives in the fields, *M. domesticus* is found only inside of houses (B. Petrov, personal communication). In Morocco and Spain, I found this species only in barns and farm houses, but not in adjacent croplands where *M. spretus* was abundant. In England, *M. d. domesticus* is found indoors as well as outdoors in wastelands and agricultural fields where it is the third most abundant rodent (Southern and Laurie, 1946). In both Spain and Great Britain, this species can be found living in a completely feral condition on small coastal islands, where they are frequently the only rodent species present (Sans-Coma and Mas-Coma, 1978; Berry, 1970). Unusual commensal habitats occupied by this species include coal mines (Philip, 1938) and frozen meat lockers (Mohr and Dunker, 1930; Laurie, 1946). Based on a lack of reports, it appears that *M. domesticus* does not enter woodland habitats in Europe. The closely related *M. poschiavinus* appears to occur only inside of buildings, and not in agricultural lands in the Poschiavo and Valtellina valleys of Switzerland and Italy (R. Sage, observations).

Within their introduced range, *M. domesticus* lives in an even greater variety of environments. This species only lives inside of buildings, not in adjacent farmland or native forests in Ghana (Jeffrey, 1977). In North America, they may be obligate commensals or live in native or introduced plant communities, but here too they are absent from some habitats. Throughout the temperate regions of the continent, these mice are found in association with human dwellings, but in different regions they may be present or absent from agricultural lands and other plant communities. Smieth (1940) reports mice as abundant throughout the settled portions of Nova Scotia, living permanently in marshes and fields in cultivated areas. Around Michigan and nearby Canada, they are abundant in farm buildings and uncommon or absent from agricultural lands (Petras,

1967a; Reimer and Petras, 1968). A comprehensive study of an entire county in Indiana showed house mice present in grasslands and cultivated areas, but absent from woodlands, river bottoms, and brush habitats (Whitaker, 1967). They are residents of the old-field successional community in North and South Carolina (Caldwell, 1964; Massey and Vandenbergh, 1980) and live in native vegetation on some coastal islands in North Carolina (Engels, 1948). In the deserts of southwestern United States, the presence of mice in native habitats is restricted and dependent in part on moisture regimes. Whitford (1976) found a permanent population in a playa grassland (*Panicum obtusum*) community, but absent from the nearby, more arid creosote (*Larrea*) habitats in New Mexico. Justice (1962) found house mice only in agricultural lands in Arizona and absent in the undisturbed native plant communities. In California, where many studies of house mice have been conducted, the local distribution of the species is well-understood. They live permanently in salt marshes (Breakey, 1963), in introduced annual grasslands (Pearson, 1963), and in agricultural lands (Myers, 1974), but they are transient or absent in coastal-scrub communities (Meserve, 1976) and oakwood and coniferous forests (W. Z. Lidicker, Jr., personal communication).

What little is known about the distribution of this mouse in South America is impressive for its altitudinal scope. Koford (1968) reported them living in the Sechura desert of coastal Peru. On a transect up into the Peruvian Andes mountains, mice were collected from houses all the way to an elevation of 4750 m (15,600 feet) (Harland, 1958). This seems to be the highest elevation at which house mice have been reported. They are permanent residents of the grassland–wheatfield ecosystem of eastern Argentina, where they may become the dominant rodent species (de Villafañe, *et al.*, 1977).

Mus domesticus is widely distributed on Atlantic and Pacific oceanic islands, which they colonized from the first sailing ships. In tropical waters they were absent from the Hawaiian islands when Cook first landed in 1778, but they were reported as resident as early as 1825 (Tomich, 1969). Presently they occur on all of the major islands in this chain. They are abundant in sugar cane and pineapple fields and also live in the forest to 2950-m (9200 feet) elevation. They were reported from the summit of Mauna Kea volcano at an elevation of 3780 m [12,400 feet]. In the Mariana, Caroline, and Marshall Islands, they live outdoors in disturbed vegetation (Baker, 1946; Marshall, 1962; Berry and Jackson, 1979). Nicholson and Warner (1953) found mice present in short and tall grass savannah and in bracken heath, but absent from wooded areas where *Rattus rattus* was most abundant in New Caledonia. The mice occur on more temperate and even circumpolar islands. In the Bering sea, they live in houses and in vegetation away from human settlements on the Pribilof islands (Preble, 1923), but are absent from further north on St. Lawrence Island (64°N) (Rausch, 1953). They live in natural environments throughout New Zealand, including the native silver beech (*Nothofagus menziesii*) forest and tussock and scree habitats on the high mountains (Taylor, 1978). Some sub-Antarctic islands support permanent populations of mice dwelling in the native scrub and heath vegetation (Berry and Peters, 1975; Berry *et al.*, 1978, 1979).

The occupation of the Australian continent has been very impressive, and it demonstrates the extent to which one species may enter a great array of habitats. Besides its ubiquitous occurrence in buildings and agricultural lands, mice now live permanently in many native environments. In southeastern Australia they occur in reed beds along river courses, heath communities, and early post-fire successional vegetation (Newsome, 1969b; Braithwaite *et al.*, 1978; Newsome *et al.*, 1975). A long-term study of the mammal fauna of the central desert regions demonstrated that *M. domesticus* was the dominant rodent species in the *Acacia* woodland, shrub steppe, and sand-dune desert communities (Newsome and Corbett, 1975). Only in the Mitchell grass plains, where *Rattus vilosissimus* was present, were mice absent. During a severe drought period and when their populations were at an otherwise very low density in most areas, *Mus* were found in high densities in the rocky gorges of a desert mountain range. Working in three forest communities in northeastern Australia, Suckling and Heislers (1978) found mice present in an introduced pine plantation and in a mixed pine–eucalypt forest along a river, but absent from a mature eucalypt forest. In western Australia, mice comprise the dominant vertebrate species in a *Banksia attenuata* woodland (Davidge, 1979) and in the native vegetation on Dirk Hartog island (Burbidge and George, 1978).

C. Food Habits

House mice are best known because of their consumption of human foods. Actually, few quantitative studies have been done on their diets. Southern (1954), in his discussion of the control of mice, described the depredations of *M. domesticus* on food stores in dwellings and agricultural fields. Commensal mice sampled a very wide variety of food items in warehouses and markets, but showed preferences for particular classes of food. Cereal grains and their derivatives, such as flour and noodles were preferred over foods containing fats and proteins (lard, butter, wax, and nuts). Items of minor preference included sugar, chocolate, and dried fruits. They ignored the seeds of legumes. Rowe *et al.* (1974) performed a quantitative study of the food preferences of commensal mice and confirmed the earlier impressions of Southern (1954). Canary seed (*Phalaris canariensis*), followed by oatmeal, was greatly preferred to a large array of alternate items such as sunflowers, peanuts, and chocolate. Mainairdi *et al.* (1975) reported simi-

lar results in experiments on Italian *M. domesticus*. While commensal *M. domesticus* may forage among a variety of foods when these are available, under extraordinary conditions they can live on a single food resource. Laurie (1946) describes colonies of mice subsisting entirely on frozen meat in food lockers. Linduska (1942) described how mice selectively attacked and ate the larvae of pea weevils (*Bruchus pisorum* L.) from infested pods, and their specific attack on the bases of cucumber flowers was noted by Foster (1977). The estimated energetic demands of *M. domesticus* under field conditions ranges from 0.42 to 1.14 kcal/g/day (Pulliam *et al.*, 1969).

Among the aboriginal species, only the diet of the mound-building *M. hortulanus* is well-known. Throughout its range in Austria (Festetics, 1961), Yugoslavia (Mikes, 1971), Rumania (Hamar, 1960) and the Ukraine (Naumov, 1940), *M. hortulanus* is a granivorous species. Seed heads of foxglove (*Setaria* sp.) are the principal items found in the food storage mounds. In agricultural fields, they store smaller proportions of the planted grains, including corn (*Zea mays*) and wheat (*Triticum* sp.). Mikes (1971) and Hamar (1960) report that insects made up less than 7% of the diet. Kochija (1960) remarks that *M. abbotti* is granivorous in southern Georgia, (S.S.R.). In Japan, *M. molossinus* eats household foods when living indoors, but lives on seeds of crop and weed species when living outdoors (Hamajima, 1962a).

Feral *M. domesticus* have a varied diet, and the available data indicates that insects are an important component. Berry and Tricker (1969) report that this species eats more animal matter than vegetable material and that they were considerably more carnivorous than the sympatric field mouse (*Apodemus sylvaticus*) on Foula in the Shetland islands. Quantitative studies of the feeding habits of mice in their introduced range show that insects form a substantial part of the diet. In Vigo county, Indiana, data on mice collected from agricultural fields from 1962 to 1965 (Whitaker, 1966) and 1970 to 1974 (Houtcooper, 1978) indicates that regular seasonal changes take place in the diet (Table I). Insects (primarily Lepidoptera larvae) are important food resources during the spring and summer, when they are most abundant, and seeds of crops and weeds predominate during the colder times of the year. This diet differed markedly from that of the sympatric white-footed mouse, *Peromyscus maniculatus,* which ate much more plant material (Whitaker, 1966). Kami (1966) found that in the sugarcane fields of Hawaii mice eat insects to a much greater degree than do the two sympatric rat species (Table I). In nearby native vegetation, selection of insects remained high (Kami, 1966). The mouse exhibits geographic variation in food habits in Australia (Watts, 1970; Watts and Braithwaite, 1978; Cockburn, 1980). In the deserts of central Australia, they were reported to eat more seeds (60% by volume) than insects (20%), but they are more insectivorous in the mesic habitats of southern Victoria. From early spring (August) until autumn (May), insects comprise more than 50% of the diet, and in the summer they form 85–100% of the food resource. At other times of the year fungi and moss sporangia predominate, and seeds comprise only a minor fraction of the diet.

Table I

Seasonal Variation and Species Differences of Important Food Types in the Diet of *M. domesticus* in Indiana and in Three Species of Rodents in Hawaii[a]

Location	Spring	Summer	Autumn	Winter
Vigo Co., Indiana				
Insects	37.1[b]	22.3	10.7	2.1
	10.3[c]	30.1	12.7	3.2
Corn (*Z. mays*)	16.4	5.2	7.4	23.9
	34.0	9.6	10.6	41.8
Seed (*Setaria* sp.)	5.9	11.1	26.9	24.5
	—	18.0	38.9	33.0

	M. domesticus	*R. exulans*	*R. rattus*
Hamakua, Hawaii			
Insects	32.0[d]	8.6	11.9
Sugar cane	9.8	67.2	59.7
Grass seeds	38.8	6.0	4.4

[a] Values represent amounts expressed as percent of volume.
[b] Whitaker (1966).
[c] Houtcooper (1978).
[d] Kami (1966).

D. Interspecific Interactions

1. Competitors

Possible competitive interactions between house mice and the other rodents have not been well studied in their native range. Berry and Tricker (1969) argue that the field mouse (*A. sylvaticus*) caused the extinction of a distinctive form of *M. domesticus* on St. Kilda Island. They hypothesize that after people left the island the *Mus* lost some competitive advantage over *Apodemus,* which was associated with human activities. Their decreased fitness gradually resulted in the decline and disappearance of the mice from the island. In the introduced parts of its range, more attention has been paid to the possibilities of competitive interactions of *M. domesticus*. Perhaps this raised sensitivity of ecologists to this question is because the house mice are foreign components in the ecosystems. In any case, many claims of interspecific interactions between the native mammals and introduced *M. domesticus* have been made. The best-studied case involves house mice and the vole (*Microtus californicus*) in the grassland ecosystems of California. This was most dramatically suggested during a study by Lidicker (1966), who observed the decline and extinction of a

sizeable population (approximately 12,000 individuals) of mice within 1 year after the introduction of a few voles onto an island study area. On the nearby mainland, DeLong (1966, 1967) studied two enclosed populations of mice in which the voles were absent from one of them but not the other. He showed that body growth rate, percentage of lactating females, and postweaning survivorship was the same on both grids. But both DeLong and Lidicker observed that postnatal, preweaning survivorship of young *Mus* was very low in the presence of *Microtus*. Quadagno (1968) also reported poor survivorship and extinction of mice on a study plot with many voles. The exact nature of this interaction between two species, which have very different food habits, is related to the social dominance of *Microtus* over *Mus* and their similar needs for burrows and nest sites. Lidicker (1966) found that *Microtus* dominated house mice in 94% of the observed encounters in cages. Seven of 8 female mice lost their week-old litters when a vole was placed in the cage (DeLong, 1966). Some of the females abandoned their nestlings immediately after the *Microtus* began to explore the burrow system.

In the southeastern United States, house mice are feral in the agricultural fields and on some of the coastal barrier islands. Based on the results of supplemental feeding and habitat manipulation experiments, Briese and Smith (1973) concluded that the old-field mouse (*Peromyscus polionotus*) excludes house mice from burrow systems and will drive them out of their preferred habitat. Only after the fields were plowed and brought back to the beginning successional stage and the *Peromyscus* had left, could the *Mus* re-establish themselves. They also report the disappearance of house mice from a barrier island following the introduction of *P. polionotus*. Thus, two cases suggest that the negative interaction between *M. domesticus* and native species centers around a burrow system, rather than a food resource. Using a correlation analysis approach, Whitaker (1967) tried to assess the degree of association and abundance between house mice and three native rodent species in Indiana. Apparently *Peromyscus leucopus* lowers the abundance of *Mus* when they live together but, interestingly, there was no interaction between the mouse and the vole *Microtus ochrogaster*. Depending on the type of habitat, the interactions varied between *Mus* and *P. maniculatus*. Sheppe (1967) studied house mice and *P. maniculatus* on a farm in British Columbia. Both species occurred in buildings, but only the latter was found out of doors. Within buildings the two species tended to live in different areas. As an experiment, the house mice that occupied a feed shed were removed by trapping. After only one day the *Peromyscus* moved into the shed. This implies that house mice were able to exclude the native rodent from only some commensal microhabitats. On the Sechura desert of coastal Peru, Koford (1968) reports that house mice were excluding a native mouse (*Phyllotis gerbillus*) from the less arid portions of the area.

In Australia, the native small mammal fauna is comparatively depauperate in species and numbers, and here *M. domesticus* lives in all types of natural habitats. It does appear that the native rodents exercise some effect on the mice: Newsome and Corbett (1975) showed a negative association between *Mus* and the abundance of other native rodents in the central desert region. In the lowland heath communities of southwestern Australia, Braithwaite *et al.* (1978) suggest that house mice occupy the food niche and replace the insectivorous, marsupial mouse species (*Antechinus*) whenever local populations become extinct.

House mice are widely distributed in the native vegetation of New Zealand, where there is no native rodent fauna. Taylor (1978) suggests that the mice are displacing an earlier immigrant species, the polynesian rat (*Rattus exulans*), from some of the habitats. But on the small, peripheral islands of that area, where mice were known to have been introduced, they are now absent wherever Norway rats (*R. norvegicus*) are present.

The general impression derived from this largely anecdotal body of information is that *M. domesticus* frequently has negative interactions with other rodent species, both in its native and introduced ranges. The nature of these interactions most frequently involves nest sites (e.g., *M. californicus* and *P. polionotus*) but may also involve competition for food resources (e.g., *Antechinus* species). More experimental studies should be undertaken (similar to those of Lidicker and DeLong) with other species within the native range of *M. domesticus* to determine how social interactions participate in limiting the width of the ecological niche of this species. The behavior of the aboriginal species in social interactions with other sympatric species would be very interesting to study, and it might show what the ancestral state was like prior to the adoption of commensal behavior in *M. domesticus*.

2. Predators

The importance of predators in controlling mouse populations has been of interest for a long time. The domestic cat historically has been considered as a major means to control house mice, and it is now known that they will continue to catch mice after both species have reverted to a feral existence (e.g., in California, Australia, and New Zealand). Early (900 AD) Welsh records fix the price of cats based on their mouse-catching experience, and the punishment for killing one of the cats in the chief's granary was a sheep and her lamb or sufficient grain to cover the dead animal when it was suspended by its tail off of the floor (Berry, 1970). Although cats may regulate the numbers of mice in some cases, they do not completely eliminate mouse populations from most habitats. They do have the ability to alter frequencies of coat color genes through selective predation (Sec. III,B).

Generally mice seem to be suitable food objects for most small predatory snakes, mammals, and birds, but no single predator species is known to specialize on mice as its primary food source. Lists of species known to prey on wild *M. abbotti,* and *M. hortulans* are provided by Kochija (1960), Naumop (1940), Hamar (1960), and Mikes (1971). The barn owl (*Tyto alba*), across its nearly worldwide range, takes house mice as a regular part of its diet. Schmidt (1970, 1975) studied the prey items found in the regurgitated pellets of barn owls from many localities in Europe and from the long-eared owl (*Asio otus*) in Hungary. It was noted that house mice were of lowest importance as prey (0–8%) in northwestern Europe, but increased in percentage (2–30) in owls living in Spain and eastern Europe. The author comments on the fact that this change in diet reflects the presence of "outdoor" mice in the south and east. Camacho (1975) also found barn owls taking many house mice (38% of the total prey items) in central Spain, but did not distinguish between the sympatric *M. domesticus* and *M. spretus* in the samples. With our better understanding of the distribution of mouse species in these areas, it is likely to be shown that owls feed more heavily on the wild species (*M. spretus, M. hortulanus* and *M. abbotti*) than they do on the sympatric and commensal *M. domesticus* and *M. musculus*. In the British Isles, mice are found in 46% of the regurgitation pellets cast up by this owl species, but they provide less than 10% of the food by weight (Berry, 1970). On a Spanish island, Sans-Coma and Mas-Coma (1978) found barn owls to be the principal predator on feral *M. domesticus*. Near the city of Davis, California, Evans (1949) studied a barn owl that ate more than 283 house mice in the course of one year. In Chile, the barn owl and white-tailed kite (*Elanus leucurus*) prey on *M. domesticus* (Jaksić and Yañez, 1979; Meserve, 1977; Schlatter *et al.*, 1980). They comprise only 10% of the owl diet, and were under-represented with respect to their abundance in the fields. The mice were the second most important prey species (8–34% of prey items) for the kites. Australian barn owls prey heavily on *M. domesticus* (Morton, 1975). During the height of mouse plagues in southern Australia barn owls move into the areas and feed principally on the mice (Morton and Martin, 1979).

Despite these observations, the role predators play in the regulation of mouse populations is not always clear. In their studies of declining or fluctuating mouse populations in California, Lidicker (1966) and DeLong (1967) did not consider predation an important factor in explaining the observed fluctuations in mouse numbers. In the same area, Pearson (1964) noted that while feral cat predation accounted for more than 80% of the production of voles (*M. californicus*) on a grassland study area, they took less than 10% of the mice. On the other hand, in a nearby area, Newsome *et al.* (1976) felt that the decline of mice on their study area during the breeding season was the result of heavy predation by raptors and other predators. In New Zealand, Fitzgerald (1978) found feral cats eating *Mus* at levels reflecting the abundance of mice in the fields. Whether the predators can or do affect the numbers of mice depends on the complex interaction between the feeding patterns and abundance of predators and simultaneously, the growth of the mouse population itself. Hall (1927) felt that the intensive predator control program that took place in 1925 was a major factor resulting in the enormous mouse plague that subsequently appeared in 1926 and 1927 at Buena Vista Lake, California. As an explanation for the fact that mouse plagues appear in the Australian region only after at least 2 years of drought conditions, Saunder and Giles (1977) suggest that the climate more severely affects the predator populations than the prey (mice). Thus under favorable conditions for reproduction, the mice are able to increase without interference until they reach levels where predators are not effective as regulators. It is clear that once mice reach plague numbers predators may increase and take many mice (Hall, 1927; Piper, 1928; Newsome and Corbett, 1975; Morton and Martin, 1979); but the eventual decline of these plague populations already seems to be underway for reasons related to reproduction inhibition (Sec. VI,B,2). Both Pearson (1964) and Newsome and Corbett (1975) feel that continued heavy predation at the end of such population booms results in an even-lower prey population level than if the predators were absent. Perhaps the action of predators in normal times prohibits mice from occupying environments that, other than being open enough to allow easy predation, would offer the necessary food resources for additional mouse populations.

3. Parasites and Diseases

Laboratory mice serve as experimental hosts for a great variety of parasitic agents. But some of these agents apparently do not occur naturally in mice. The tapeworm, *Taenia crassiceps,* for example, is routinely passed through lab mice in studies of the immune response (Smyth, 1969), but its primary natural hosts are foxes and native North American rodents (Freeman, 1962). On the other hand, the occurrence and behavior of some well-studied mouse pathogens, such as mouse ectromelia (Fenner, 1949) are poorly known in the wild. Even though some parasites of mice are known vectors for human diseases (Cameron, 1949), I found little systematic effort to study mice in relationship to their parasites and diseases (Table II). I have used the term "parasites" in its broadest meaning: to encompass both proto-organisms, e.g., intracellular viral genomes, and more conventional animals such as ticks and fleas.

Although relationships between parasites and wild mice do not appear to be well-studied, some conclusions can be made

Table II

Records of Parasites Found in House Mice

Species	Locality	Findings	Reference
Intracellular parasites			
M. hortulanus	U.S.S.R.	A neurotropic virus, similar to the virus of tick-borne encephalitis was isolated in animals of this species	Kalabukhov and Subladze, 1946 (cited but not referenced in Mikeš, 1971)
M. musculus (?)	Turkmen, U.S.S.R.	Four species of *Eimeria* (*E. falciformis, E. hindlei, E. krijgsmani,* and *E. paragachica*) found	Glebezdin, 1974
M. musculus (?)	Eastern Europe	In 487 animals from many European localities, only 1/28 specimens from Macedonia tested positive for *Babesia microti*	Sebek *et al.*, 1977
M. musculus	Poland	12% of 140 mice tested positive for *Toxoplasma gondii*. This was the highest frequency to occur among seven rodent species examined	Slowakiewicz *et al.*, 1972
M. musculus	Czechoslovakia	Isolated a highly pathogenic rabies-like virus from two specimens	Sodja and Matouch, 1972a,b
M. domesticus	California	Only 1/93 mice reported positive for western equine encephalomyelitis virus, and 1/51 were postive for St. Louis encephalitis arborvirus	Hardy *et al.*, 1974
M. domesticus	California	Reports high incidences of endogenous C-type mouse leukemia virus, lymphocytic choriomeningitis, polyoma virus, and cytomegalovirus in some of 15 populations studied	Gardner, 1978
M. domesticus	California	Studied populations with high and low incidences of polyoma virus and determined that this virus does not normally cause tumors in wild animals	Gardner *et al.*, 1974
M. domesticus	California	Found the provirus genome of mammary tumor virus present in variable amounts	Cohen and Varmus, 1979
M. domesticus	California	Identifies, as *Bacillus murispeticus,* a pathogenic agent taken from dying house mice at Buena Vista Lake	Wayson, 1927
M. domesticus	Australia	Found no signs of mouse pox (infectious ectromelia) in 150 wild mice from the Melbourne region	Fenner, 1949
M. domesticus	Australia	Only 2/141 animals had *Sarcocystis*-like organisms	Munday *et al.*, 1978
M. domesticus	Pennsylvania and Hawaii	Notes positive serological responses in 58% of 170 Hawaiian mice for *Leptospira* sp.; also reports a positive test in Pennsylvania	Minnette, 1964
M. domesticus	Illinois	Mice tested positive for *L. ballum* but not for *L. icterohemorrhagiae*	Schnurrenberger *et al.*, 1970
Nematoda			
M. domesticus	France	Pronounced sex differences in prevalence of *Aspiculuris tetraptera*	Roman, 1951
M. domesticus	England	No nematodes found in 35 mice caught in the Outer Hebrides Islands	Elton, 1934
M. domesticus	England	Studied 43 wild mice and found that all carried pinworms (*Trichuris muris*)	Behnke and Wakelin, 1973
M. domesticus	England	In 102 mice, only *A. tetraptera* and *Syphacia obvelata* were found	Behnke, 1975
M. domesticus	Indiana	*Heligmosmoides polygyrus, Protospirura* sp., and *Syphacia* sp. were found in decreasing order of frequency in a sample of 503 feral mice. Only *Aspiculuris* sp. was found in a sample of 66 mice taken from a building. In 180 mice two species of nematodes were found in high frequencies: *S. obvelata* (49%) and *A. tetraptera* (40%)	Whitaker, 1970; Clark, 1970; Adalis and Scherich, 1970
M. domesticus	Hawaii	Only 3.6% of 720 mice contained stomach nematodes identified as *Protospirura* sp.	Kami, 1966
Platyhelminthes			
M. domesticus	Egypt	33% of 108 mice contained cestodes belonging to six species. The cat tapeworm (*Taenia taeniaformis*) was most abundant. The cestodes *Hymenolepis diminuta* and *H. nana fraterna* were common	Fahmy *et al.*, 1969
M. domesticus	U.S.A.	1% infestation with the hydatid, *Echinococcus multilocularis*	Leiby *et al.*, 1970

(continued)

Table II—*Continued*

Species	Locality	Findings	Reference
M. domesticus	Indiana	9% of 503 feral mice contained cestode infections	Whitaker, 1970
M. domesticus	Hawaii	The cat tapeworm (*T. taeniaformis*) was common	Alicata, 1969
M. domesticus	Ponape Island	Only three of 175 mice had *Capillaria* worms	Marshall, 1962
Siphonaptera			
M. hortulanus	Rumania	Mentions four species of fleas occurring on mice: *Ctenophtalmus assimilis, C. rettigi, C. segundus,* and *Stenoponia tripectinata*	Hamar, 1960
M. hortulanus	Yugoslavia	Found *C. assimilis, S. tripectinata, Leptopsylla segnis,* and unidentified specimens of the family Ceratophyllidae	Mikes, 1971
M. musculus	Amur, U.S.S.R.	On 11,000 mice only *L. segnis* and *Rhadinopsylla integella* were common	Chernykh and Kozlovskaya, 1976
M. musculus	Poland	Found five species on 29 mice, including: *Ctephtalmus agyrtes, C. assimilis, Ceratophyllus fasciatus,* and *C. turbidus*	Lachmajer and Skierska, 1957
M. musculus	Poland	During an 8 month study of marked animals, found eight flea species. Common ones include: *L. segnis, C. agyrtes,* and *C. turbidus*	Janion, 1961
M. musculus	Poland	Only four species were found on 45 mice, including *L. segnis* and *C. agyrtes*	Haitlinger, 1974
M. domesticus	Egypt	Four species of fleas found on 108 mice, including *Xenopsylla cheopis,* and *L. segnis*	Rifaat *et al.*, 1969
M. domesticus	England	Only *C. agyrtes* and *C. fasciatus* found in an Outer Hebrides Islands sample	Elton, 1934
M. domesticus	Indiana	Only 2/470 field-living mice had fleas	Whitaker, 1970
M. domesticus	Hawaii	In large sample of mice, found five species including: *Ctenocephalides felis, L. segnis,* and *X. cheopis*	Alicata, 1969
Acarina			
M. hortulanus	Rumania	Five species of mites are mentioned: *Haemogamasus nidi, Haemolaelaps glasgowi, Hirstionyssus musculi, Laelaps algericus,* and *L. muris*	Hamar, 1960
M. hortulanus	Yugoslavia	Two species of ticks (*Dermacentor marginatus* and *Ixodes ricinus*) and seven species of mites were found on these animals. Common species include: *H. glasgowi, L. algericus, L. agilis, Eulaelaps stabularis,* and *H. nidi.* Seventeen species of mites were found in the nest material	Mikes, 1971
M. musculus	Amur, U.S.S.R.	Mites were very uncommon. Most abundant species included *E. stabularis, H. glasgowi, L. pavlovski, Ornithonyssus bacoti,* and *Allodermanyssus sanguineus*	Chernykh and Kozlovskaya, 1976
M. domesticus	England	Eleven species of ticks and mites found on 35 mice and in their nest materials in the Outer Hebrides Islands, including *E. stabularis* and *Myobia musculi*	Hora, 1934
M. domesticus	New York and Illinois	The mite vector for rickettsialpox *A. sanguineus* was found on wild mice	Pratt *et al.*, 1949
M. domesticus	Indiana	From 428 mice, eleven species of mites were reported. The 5 most common species were: *M. musculi, Radfordia affinis, Mycoptes musculinus, O. bacoti* and *Androlaelaps fahrenholz* (=*H. glasgowi*) Alicata, 1969	Whitaker and Wilson, 1968
M. domesticus	Hawaii	Five species of mites were reported: *E. stabularis, Listrophorus musculus, M. musculinus, M. musculi,* and *R. affinis*	

from the scattered literature. It is apparent from the array of organisms listed in Table II that house mice do support a great variety of parasites. However, some taxonomic groups seem to be absent from mice. In a large series of Hawaiian *M. domesticus,* Alicata (1969) found no *Trichina* worms, despite their presence in the local rat populations. No cestodes of the genus *Taenia* were present in 175 mice from Ponape Island, although this parasite was very common in rats (Marshall, 1962). Trematodes do not seem to be common in mice (Fahmy *et al.*, 1969; Clark, 1970). Acanthocephalans were looked for, but not found, in mice from Egypt, Indiana, and Ponape Island (Fahmy *et al.*, 1969; Clark, 1970; Marshall, 1962).

Sarcocystis-like organisms do not seem to be frequently reported from mice, but I found cysts of this type in wild-caught *M. abbotti* from Macedonia and in *M. domesticus* from Egypt. In view of the widespread predation on house mice by the barn owl (Sec. II,D,2) and the ease with which *Sarcocystis* oocytes from owls encyst in lab mice (Cerna, 1976, 1977), it seems peculiar that this relationship between predator and prey has not been more fully studied.

Whether there are taxonomic or geographical differences of parasites among members of this complex is not clear. Gardner (1978) mentions that the ecotropic and xenotropic, murine leukemia viruses of *M. molossinus* from Japan and *M. domesticus* from California are only partially related, based on DNA sequences. One can see from Table II that some specis of fleas, such as *Leptopsylla segnis,* occur on all species of house mice for which there are data. Some parasites of *M. domesticus* have traveled with this animal from its native range into new habitats, e.g., *Xenopsylla cheopis* and *L. segnis* in Egypt and Hawaii and *M. musculi* in England, Indiana, and Hawaii (Table II). The extent of this spread of parasites from the native range into invaded areas is not understood at present.

Not recognizing the correct identity of species of house mice is liable to produce misunderstandings in biomedical research. In the lands where *M. domesticus* has been introduced, this is not a problem, but in areas where aboriginal and commensal forms coexist this could result in erroneous conclusions about the danger of mice to human health. This seems particularly true in the Soviet Union, where considerable effort has been made to study mice in relation to diseases such as plague. Zemskaya (1973) describes mites and the viruses and bacteria isolated from them [including lymphocytic choriomeningitis virus (LCM), *Yersinia pestis* and *Rickettsia akari* (rickettsial pox)], which are ostensibly found on "*M. musculus.*" But from the studies of Hamar (1960) and Mikes (1969, 1971), we know that it is the aboriginal species, *M. hortulanus,* and not the sympatric commensal, *M. musculus,* that harbors large numbers of the important species of mites, which act as vectors for the pathogens. This same kind of confusion about the identity of host species of mice is probably true of the reports of coccidian parasites (Glebezdin, 1974) in Russian mice and babesiasis in mice of eastern Europe (Šebek *et al.,* 1977). The discussion by Lankin (1978) of plague epizootiology and mice probably confuses wild *M. abbotti* and a commensal species.

Sometimes there are small-scale geographical differences in infestation rates, and these might affect the ecological characteristics of local mouse populations. In a study of the natural history of polyoma virus, Rowe *et al.* (1961) examined *M. domesticus* from four boroughs of New York City. They found a very patchy distribution of the virus: carriers were present in only one district, and within that area only on 7 of 26 blocks. Yet, infestation rates on these blocks were high ($\bar{X} = 0.18$; range = 0.08–0.38). Even at this scale, there was microgeographic heterogeneity: viral foci were present on some, but not all floors of an apartment building. Since the virus is most effectively transmitted to the young mice during lactation, it is reasonable to assume that these infected populations are the descendants of single, female colonists. Also, Emmons *et al.* (1978) found LCM patchily distributed in mice from the San Francisco Bay region of California. A flea index, measuring levels of infestation on *M. domesticus,* was lower around the port areas of Suez, Egypt, than in the nearby desert settlements (Mahdi *et al.,* 1970). Comparing samples collected in fields versus buildings, Clark (1970) observed major differences in the nematode and mite species parasitizing *M. domesticus* in Indiana.

Generally, it appears that *Mus* species support fewer parasites than many other rodents. In both Indonesia and India, *M. castaneus* had very low levels of flea infestations compared to sympatric species of rats (*Rattus* sp.) and the bandicoot (*Bandicota* sp.) (Hadi *et al.,* 1976; Srivastra and Wattal, 1973). Haitliner (1974) contrasted the lower level of flea infestation on *M. musculus* to *Microtus* and *Apodemus* species in Poland. Egyptian *M. domesticus* had a lower flea infestation than two species of *Rattus* (Rifaat *et al.,* 1969). Elton (1934) states that *M. domesticus* had fewer fleas than field mice (*A. sylvaticus*). Infestation with stomach nematodes was 3.6% in *M. domesticus* versus 36% in *R. rattus* in field populations in Hawaii (Kami, 1966). But in the same area *Leptospirosis* organisms were detected in higher frequency in mice than in three species of *Rattus* (Minnette, 1964).

Another result emerges from the available studies: parts of the mouse population are differentially affected by parasites. In Polish *M. musculus* (Janion, 1961) and Egyptian *M. domesticus* (Rifaat *et al.,* 1969; Mahdi and Arafa, 1971), it was observed that the male portion of the population had more fleas than females. In English *M. domesticus,* the males generally have more whipworms and pinworms (*Trichuris muris* and *Aspiculuris tetraptera*) than females (Behnke and Wakelin, 1973; Behnke, 1975). This relationship was temporarily altered in pregnant females, who supported higher worm burdens than males or nonpregnant females. Roman (1951) observed the same phenomenon of a greater burden in males (*M. domesticus*) of *A. tetraptera* in France. A comparison of parasite loads between field- and house-dwelling mice in Indiana showed that in both habitats the males had a higher incidence and a greater infestation than females. This was despite the fact that different species of mites predominanted in the two environments (Whitaker, 1970; Clark, 1970). With respect to the endoparasites of these same mice, a different pattern prevailed: while the incidence of nematodes was identical in both sexes the male field mice and the female house mice had higher infection levels than the opposite sex from the same habitat. This reversal in infection levels between the sexes may reflect different ecological patterns in these two habitats, alternate

strategies by different species of nematodes, or perhaps a higher number of pregnant females in the March–April sample of house-dwelling mice versus the year-round sample of field mice. Whitaker (1970) and Behnke (1976) showed seasonal and age-dependence differences in parasite loads in the feral mice, but this may be a fortuitous correlation with annual changes in the demographic structure and density of the mouse population. Similar relationships between parasites and different sex, social, and age classes of animals were shown in laboratory strains (Mathies, 1959a,b; Stahl, 1962).

From these findings in both wild and domestic mice, we can conclude that this variability in parasite load is a typical aspect of the biology of these animals. Behnke (1975) suggests that nonpregnant female mice may have a more effective immune response system and can reject the parasites or retard their ability to mature. It is known that viral carcinogenesis is enhanced in laboratory mice by immunosuppression treatments (Allison, 1970). Perhaps the condition of the immune-response system of the mouse in large part determines its ability to withstand and survive parasite attacks and contribute to the next generation. Experimental manipulation of wild mouse populations with immune suppressing drugs might show how important this cell system is to the survival of free-living populations or, conversely, what role parasites and disease play in population regulation.

A virus which causes an order of magnitude increase in the concentration of lactate dehydrogenase is reported from wild *M. domesticus* from Germany, England, the United States, and Australia (Rowson and Mahy, 1975). The virus, called lactic dehydrogenase virus (LDV), does not cause any clinical disease in mice, and produces only minor histological changes in the spleen and lymph nodes. But, there is an altered response to infectious agents and the development of tumors. A life-long viremia results from infection, but the virus is not readily passed between mice. The dynamics of the virus in wild populations is poorly known, but the limited data suggests that levels of infection are very high. Rowson (1980) reports that LDV will replicate only in species of the genus *Mus*.

More insight into the interaction of parasites and wild mice comes from the detailed studies of C-type retrovirus viruses by Gardner (1978). Some populations of *M. domesticus* from various regions in southern California carried endogenous, murine luekemia virus (MuLV). The Lake Casitas (LC) population of mice was studied in detail, and here it is possible to make conclusions about the effect of the viruses on their hosts. From his studies, it has been shown that three classes of virus are present: amphotropic (A-tropic), ecotropic (E-tropic) and xenotropic (X-tropic). They vary from one another in their range of host cells and similarity of DNA. These viruses may produce spontaneous lymphomas and paralytic disease in wild mice. Mice carrying these viruses demonstrated either a low or high expression of virus particles and had a corresponding susceptibility to spontaneous tumors and lower-limb paralysis. High expressor mice were found in 2 of 15 populations sampled. The A-tropic virus is lymphogenic wheras E-tropic virus is both lymphoma- and paralytogenic, and both viruses have been in the LC population for more than 7 years. In this population, 18% of the mice will ultimately develop spontaneous lymphomas or hindlimb paralysis if they are held in captivity. Levels of enzyme variability were normal in a sample of these mice, suggesting that no severe fluctuation in numbers has taken place in this infected population (Rice *et al.*, 1980).

How can such a seemingly detrimental agent be maintained in a viable mouse population for so long? The answer lies in the etiology of the disabilities caused by the viruses. Tumors and paralysis do not become manifest in animals brought into the lab until after 5–6 months of residence, and most cases do not appear until after 1 year of captivity. Andervont and Dunn (1962) also observed that wild *M. domesticus* did not begin to develop tumors until they were older than 16 months in age. Ultimately 43% of their mice developed tumors. In a typical mouse population, there are very few mice surviving until such an age, so there is little depression of either litter production of the group or reduction in the evolutionary fitness of the individual mouse. Thus the viruses are nearly neutral in their affect on the mice. During the evolutionary history of the viruses there has presumably been strong selection to control pathogenic effects until after the host mouse has passed through most of its normal breeding period, thereby minimizing any negative affect on the real fecundity of the individual or productivity of the population. Passage of the virions in both the gametes and in the milk, ensures its successful introduction into the relatively short-lived colonies that characterize mouse populations.

Either strong co-evolution with, or adaptation to, such viruses must be taking place. In their description of the endogenous retroviruses, Callahan and Todaro (1978) point out that these viral genomes account for 0.04% of the mouse (*M. cervicolor*) DNA and represent a significant part of the cellular genome. (It is comparable to the amount of DNA used to code for the 28 S and 18 S ribosomal proteins!) Clearly, from the mouse's viewpoint something must be done to manage such potentially destructive material. The story developing from the study of MuLV suggests that just such long-term adaptation has occurred. The MuLV of the inbred strain AKR is highly leukemogenic: by 1 year of age essentially all mice of this strain have the disease (reviewed by Lilly, 1978). The proviral genome responsible for the leukemia exists in two copies on different chromosomes of this strain, and it may be present or absent in other inbred strains. Some mouse genes inhibit the development of the leukemia: Alleles at the *Fv-1* locus suppress the production of viral particles, and the *H-2* haplotype strongly influences the capacity of the mouse to respond to the malignant cells producing viral antigens. Steffen *et al.* (1980)

and Chattopadhyay *et al.* (1980) have searched for this proviral sequence in other species of the house mouse complex. In *M. spretus, M. domesticus,* and *M. musculus* the sequence was not present. It may be present in *M. castaneus,* and it is definitely present in *M. molossinus.* Interestingly, Odaka *et al.* (1978) observed that wild *M. molossinus* in Japan were able to strongly suppress the production of leukemia when challenged by Friend or AKR MuLV. They map this capability to an allele at the *Fv-4* locus. These data are consistent with the theory of the introduction of this AKR proviral genome during the hybridization events between *M. domesticus* and *M. molossinus* that established the majority of inbred strains (Sage and Marshall, in prep.). From the evolutionary standpoint, it suggests that in the native mouse population these proviral genomes are kept under control by co-adapted gene complexes. In the case of MuLV, these may include alleles at the *Fv-1* and *Fv-4* loci and the *H-2* chromosome region. With respect to this prediction, it is expected that the unique *H-2* haplotypes of *M. molossinus* (Sec. III,F) may be particularly effective in inhibiting antigens of AKR MuLV. Under this evolutionary model, it is predicted that the many other "silent" proviral genomes found by Steffen *et al.* (1980) represent agents kept under control by a complex of mouse genes produced by natural selection to minimize tumor growth in young mice. Only when extreme events, such as these hybridizations during the formation of the laboratory mouse, are these co-adapted complexes sufficiently disrupted to permit the pathogenic expression of cancers in mice of reproductive age. However, Gardner *et al.*(1980) recently discovered a gene (*Akvr-1*) in wild *M. domesticus* from California that restricts viremia by AKR endogeneous retrovirus, and Molony and Friend viruses. It may be that this gene is identical with the *Fv-4* gene described by Odaka *et al.* (1978) (M. B. Gardner, personal communication). If this is true then it is expected that the AKR proviral sequence will ultimately be found in *M. domesticus.*

Although mice are host to a wide variety of parasites, many which have deleterious effects on individual mice, the role of such agents in controlling mouse populations is not clear. Evidence from the field is notoriously difficult to gather in this area of study. Lidicker (1966) did not find any sick or weakened animals in a study of feral *M. domesticus.* Animals weakened by parasites are apparently consumed by predators long before the investigator can find them. But in some cases disease has been directly observed in wild *M. domesticus* populations. Pustular infections of *Pasturella pseudotuberculosis* and fungal plaques (favus) occurred on mice living in dense populations inside of a haystack (Newsome, 1971). After an enormous population increase near Buena Vista Lake in central California, sick and dying mice were found (Piper, 1928). A virulent bacterium was isolated from these mice by Wayson (1927). Sick mice described by Pearson (1963) in California were almost certainly suffering from this same pathogen. In one marked population of mice studied by DeLong (1967) in coastal California, dead animals were found and the population declined drastically in one month. The generalized mortality of this population, including all age and sex classes, differed from the more selective mortality seen in other declining populations that he studied. These two facts indicate that an epidemic of a virulent disease nearly eliminated this one population. Evans (1949) describes finding moribund and paralytic mice in a California population declining to extinction. These mice were old and may have been showing the pathological symptoms of the C-type virus discussed earlier. Thus there are direct field data supporting some role for parasites in controlling population size in mice. A general review of population control and evolution in parasites has been presented by Anderson and May (1979a,b).

III. VARIATION

A. Morphological Variation

Anatomical variation of wild house mice has been studied most frequently (1) in analyses of ontogenetic development, (2) for purposes of taxonomic identification, and (3) to detect genetic differentiation among populations and the operation of natural selection. The general development of Japanese *M. molossinus* has been covered in detail by Hamajima (1962b, 1963, 1964), and Searle (1960) reported on skeletal variation of Malaysian *M. castaneus.* Dynowski (1963) studied morphological variability in a large sample of *M. musculus* from Poland. Increasing osteoporosis and the disappearance of the Haversian canal system was observed in aging *M. musculus* from Czechoslovakia (Globocnik and Rajtova, 1978). Bader (1965) examined the degree of developmental stability in low (inbred lab strains), medium (hybrid lab strains), and highly variable (feral) *M. domesticus.* The latter two groups produced more uniform structures in comparisons of dental characters from the left and right mandibles. He suggested that genetically variable animals are better able to buffer their developmental systems from disturbance than homozygous mice. After studying patterns of wear on the molars of feral *M. domesticus* of known age, Lidicker (1966) established an index between age and tooth wear. Weber (1950) and Sans-Coma *et al.* (1979) reported on osteological variation in *M. domesticus.*

Efforts to use external morphological characters to distinguish among the European populations of *Mus* were employed by Zimmermann (1949), Ursin (1952), van de Kamp-Hilt and van Bree (1964), Serafinski (1965), and Keller (1976). Both relative tail length and the shape of the skull adequately served to identify sympatric samples of *M. domesticus* from the congeneric *M. booduga* in Pakistan (Hussain *et al.,* 1976). The

zone of contact and hybridization between *M. musculus* and *M. domesticus* in Denmark was successfully detected by Ursin (1952) using measures of relative body, tail, and foot size. But Zimmermann (1949) and Serafinski (1965) were only partly successful in their attempts to classify the European house mice based on morphological measurements. It was easy for them to distinguish the relatively large, long-tailed *M. domesticus* from the other species. Because they misunderstood the large genetic differences separating the other shorter-tailed species, they were confused by the great amount of "intrapopulational" variation, as they perceived the situation. To explain this variation in the eastern European mice, they had to invoke convoluted models of shifting adaptations to commensal and free-living habits in local areas by the mice. The existence of small populations of *M. musculus* embedded in the range of *M. domesticus* in Holland was discovered by van de Kamp-Hilt and van Bree (1964) using differences in relative tail length.

An early attempt to detect differences between local populations was made by Berry (1963). He studied a series of skeletal variants (epigenetic characters) in samples of *M. domesticus*. The animals came from different ricks (haystacks) and farms in England and from various parts of the world. Significant interrick variation in the frequencies of these variants was detected, and he explained this variation as the probable result of the origin of different rick colonies by small numbers of genetically distinctive founders. With the advent of biochemical methodologies, the use of this quasi-genetic variation for distinguishing populations has been superceded by a more precise method of genetic analysis. Van Valen (1965) looked at many of these same samples of rick mice for signs of natural selection in action. Comparing the relative width of the third molar in different individuals, he concluded that age-dependent, destablizing selection for molar width was operating in some populations. Differences in the degree of this effect were noted between populations living in ricks made up of different types of grain. He reported the decline in frequency, to apparent extinction of a dental trait in samples of mice from Skokholm Island collected over a period of years.

B. Coloration

Color variation is widespread in wild mouse populations. Searle (1968) and Silvers (1979) discuss the genetics and occurrence of the more uncommon mutants that appear in populations. Here, I consider only the variation that is of a polymorphic nature in different species of mice. The most frequent form of variation is seen in belly coloration, which is due to an allelic series at the agouti (*A*) locus, but there are other genes that modify the degree of overall darkening. In the aboriginal species *M. abbotti, M. hortulanus,* and *M. spretus,* I have not seen polymorphism in ventral colorations. Japanese *M. molossinus* are polymorphic in belly coloration, ranging from gray to white (Hamajima, 1964).

Three ventral color patterns are commonly observed in *M. musculus* (Serafinski, 1965; R. Sage, observation). There are light- and dark-bellied mice similar in general appearance to the variation to be described at the *A* locus in *M. domesticus*. There is a difference that I have noted in the patterning of the dark-bellied variant in this species versus *M. domesticus*. In *M. musculus* (and in *M. castaneus*), the dark-belly coloration has a barred appearance instead of the uniform coloration seen in *M. domesticus*. This persists in laboratory-raised animals. Based on informal breeding experiments with *M. musculus* mice from the Belgrade region, the light color is dominant to the dark color in this species, as is true in *M. domesticus* (Morgan, 1911). The third color pattern seen in *M. musculus* is a cross-shaped patch of rufous hair on the throat and chest area. Serafinski (1965) calls this the *sylvaticus* type of coloration in reference to its similarity to the pattern in the related *A. sylvaticus*. I have observed this coloration in mice from northern Denmark, Czechoslovakia, Austria, and Yugoslavia. Kaliss (1942) pictures animals with this coloration in stocks maintained by L. C. Dunn.

There are a number of color patterns in *M. domesticus,* only some of which are similar to those described for *M. musculus*. Four common color variations in this species include the light- and dark-bellied agouti series previously described, a "snow-white," and a melanic phenotype. The "snow-white" coloration is not part of the agouti series, but rather a phenotype with a multifactorial genotype (Falconer, 1947). Melanic coloration is controlled by genes on a number of chromosomes. In Europe and North Africa, all of these color patterns can be found in native *M. domesticus* populations, but there is a strong component of geography to this distribution. Melanic forms are present in high frequencies in the northwestern part of Germany and are essentially fixed in some parts of the Austrian, Swiss, and Italian Alps (Zimmermann, 1949; R. Sage, observation). A chromosomally derived form of *M. domesticus—M. poschiavinus*—was first distinguished on the basis of its melanistic coloration, and in this case the genes controlling melanism are found on five chromosomes (Radbruch, 1973). Melanic mouse populations are also found in the New World (Azores, Cuba, and Mexico), where such populations were described as separate taxonomic units (Zimmermann, 1949). The "snow-white" phenotype predominates among the desert populations of *M. d. praetextus* of Morocco, Egypt, and Israel (R. Sage, observation). A sample from the oasis of Erfoud in southern Morocco is apparently homozygous for the genes governing this phenotype, as all of the progeny that I have raised from three wild pairs of animals continue to show only this color pattern. Egyptian and Israeli populations are polymorphic for this pallid coloration. At Azrou, in the more

mesic part of Morocco and only 200 km from Erfoud, I found the *M. domesticus* homozygous for the dark-bellied condition (Chapter 2, Fig. 4).

Dark- and light-bellied *M. domesticus* are present in Europe with frequencies of the two alleles varying between regions. British mice are mostly homozygous for the dark phenotype (Berry, 1970). Schwarz and Schwarz (1943) tried to make the lighter colored mice into a recognizable subspecies (*M. d. brevirostris*) in the Mediterranean region. I collected a pair of mice from the Adriatic coastal region of Yugoslavia (Metkovič), which produced young with light- or dark-colored bellies. Subsequent breeding in the lab produced homozygous lines based on a model of simple dominance for the light-bellied, A^W, agouti allele. Although the dark-belly allele is most common in most of central and northern Europe, in sandy regions along beaches the white-belly allele may predominate. Natural selection for lighter coloration, more similar to the sandy background, may produce this change in allelic frequencies (Berry, 1970).

In North and South America, melanic variants are present, as already mentioned, but the "snow-white" coloration seems to be very rare. Eaton and Schwarz (1946) report finding one such variant in Virginia. A polymorphism for the dark- and light-belly agouti alleles is widespread (Nichols, 1944; Engels, 1948; Dunn *et al.*, 1960; Petras, 1967c; Selander and Yang, 1970). In most populations the A^W allele is low in frequency, on the order of 5–15% (Petras, 1967c). But on the barrier islands of North Carolina, the white-bellied phenotype was found in more than 80% of the mice living on the sand dunes. Both Graf (1963) and Harland (1958) mention the predominance of light-colored mice on sandy arid islands in Hawaii and lowland coastal habitats in Peru. These repeated cases of convergence to light-belly coloration in sandy environments is strong inferential evidence of natural selection determining coat color in mice.

Kaufman and Wagner (1973) showed a significant loss of albino versus agouti inbred mice left in outdoor enclosures, and attribute this to preferential predation (by owls?) on the more conspicuous white mice. But the variation in attack frequencies by corn snakes (*Elaphe guttata*) on laboratory and wild mice was attributed to the activity of the prey animals rather than to their coloration (Smith and Watson, 1972). Experiments such as the one by Kaufman (1974) on natural color variants of the old-field mouse (*Peromyscus polionotus*), but using feral house mice with the alternate agouti alleles would provide a better understanding of how this particular polymorphism is maintained in the wild. The role of predation in maintaining the agouti coloration was shown in an elegant study by Brown (1965) of a barn-dwelling population of mice in which a recessive pink-eye mutant was present. During six sampling periods extending over an 18-month period, the frequency of the pallid (homozygous) mutant fluctuated: 0.22, 0.29, 0.32, 0, 0, 0.05. In periods 1–3, there were no cats inside the barn, but during the next two sampling periods cats were present, but were again excluded before the final census was made. Cats were observed catching both the pallid and normal mice, and it is clear from these fluctuations that the conspicuous mutant was at a selective disadvantage in the presence of this visually oriented predator.

While various recessive color mutants are occasionally reported from wild mouse populations (Morgan, 1911; Nichols, 1944), their presence, even in the heterozygous condition appears to be low. Only a spotting gene seems to be widespread at a low frequency. Dunn *et al.* (1960) and Selander and Yang (1970) report finding these variants in North American *M. domesticus*. I have found it appearing in partly inbred stocks of feral *M. domesticus* (Switzerland and Morocco) and in *M. hortulanus* (Yugoslavia). Petras (1967c) noted that animals with the belly spot tended to die young or were sterile. He was unable to find any other color alleles beside the agouti series and spotting genes when he bred feral mice against lab mice recessive at seven loci affecting coloration. In two stocks of *M. hortulanus* raised in the laboratory from Austria (Halbturn) and Yugoslavia (Pančevo) a white blaze on the forehead has appeared after about three generations of inbreeding. This suggests that this color variant is widespread and in a high frequency in this species which shows a very low level of protein variation (R. Sage, observation). Deol (1970) comments on how these color mutants are frequently associated with pleiotropic effects relating to nervous system development. Nevertheless, there may be a high load of deleterious genes in some populations. Wallace (1978) reported on a sample of *M. domesticus* from a high elevation locality in Peru that has produced many lethal genes during a period of close inbreeding in the lab. The limited data on the geographical partitioning of coat coloration and low frequency of many color variants supports the idea that natural selection is operating to maintain the commonly observed polymorphisms.

C. Mitochondrial and Nuclear DNA

Yonekawa *et al.* (1980) studied the fragment patterns of mitochondrial DNA from various species of house mice using the technique of partial digestion with restriction endonucleases. Among 25 inbred laboratory strains there was no variation, and they were identical to a sample of wild *M. domesticus* from Canada. Patterns from *M. castaneus* and *M. molossinus* were quite different, and these authors estimate that the time of divergence between these forms and *M. domesticus* is about 2.5 and 1.1 million years ago. Our results (Ferris, Sage, and Wilson, in preparation) show that the inbred strains SF/Cam and IS/Cam have patterns different from the common inbred type. Furthermore, there is a great amount of variability

in mitochondrial DNA in wild *M. domesticus* and *M. musculus* populations but apparently very little in *M. molossinus*. The topology of a tree of genetic relationships derived from DNA similarities is approximately the same as the one produced from the studies of enzymes (Fig. 1).

Brown and Dover (1980) found considerable differences between the satellite DNAs of *M. spretus* and *M. domesticus:* great differences in amounts but lesser changes in the organization and sequence composition of the DNA. Rake (1974) studied the reassociation kinetics of DNA in *M. domesticus* and *M. molossinus*.

D. Biochemical Variation

With the development of improved electrophoresis and staining techniques in the early 1960s, investigators immediately discovered alternate molecular forms of proteins among inbred mouse strains. That work has continued at an ever-increasing rate, and today electrophoretically detectable differences in more than 50 proteins have been reported among lab mice. In most cases, the chromosomal position of the genes controlling these variants have been located (summarized by Womack, 1979, Altman and Katz, 1979). Two-dimensional electrophoresis promises a quantum increase in resolving power for future studies of protein variation among inbred strains and wild mice, and this search has already begun (Elliott, 1979; Klose, 1979; Racine and Langley, 1980a,b). Alternate molecular forms, differing in their resistance to heat denaturation, have been shown to exist within a single, electrophoretic mobility-class (Bonhomme and Selander, 1978a,b). This demonstrates the occurrence of even more genetic variability than is revealed through the use of only one technique of biochemical preparation.

From 1967 to 1970, investigators reported on the presence and patterns of protein variation in wild mouse populations. Most of these studies dealt with variation in *M. domesticus* in North America and England (Petras, 1967a; Selander and Yang, 1969; Petras *et al.*, 1969; Ruddle *et al.*, 1969; Selander *et al.*, 1969b; Berry and Murphy, 1970; Selander, 1970a,b; Selander and Yang, 1970; Roderick *et al.*, 1971), but Selander *et al.* (1969a) studied *M. domesticus* and *M. musculus* in Denmark. Later studies have added more information to our understanding of heterozygosity levels in *M. domesticus* populations from around the world (Berry and Peters, 1977; Sage, 1978; Rice and O'Brien, 1980; Rice *et al.*, 1980).

The earliest studies proposed a number of questions:

1. What are the overall levels of genetic variation in mice versus other organisms?
2. How are mouse populations organized on the micro- and macrogeographical scale?
3. Are there patterns of temporal variation in local populations?
4. What is the relative importance of genetic drift versus selectional processes in maintaining the observed variability?

These were to be the central themes for research by evolutionary biologists during the succeeding years (general reviews by Lewontin, 1974; Nei, 1975; Ayala, 1976), and the mouse data figured importantly in those discussions. Subsequent lines of investigation have centered on island populations of *M. domesticus* in Great Britain (Berry and Peters, 1977); in the tropical Pacific region (Wheeler and Selander, 1972; Berry *et al.*, 1981); on cold, sub-Antarctic islands (Berry and Peters, 1975; Berry *et al.*, 1978, 1979); on the nature of hybrid zones (Hunt and Selander, 1973); and on the identification of taxonomic units within the house mouse complex (Britton and Thaler, 1978; Sage, 1978; Bonhomme *et al.*, 1978a; Minezawa *et al.*, 1979; Britton-Davidian *et al.*, 1980; Sage and Marshall, in prep.).

The first extensive surveys of variation at a large number of loci (15–40) demonstrated that house mice were polymorphic at levels comparable to what is found in man, but somewhat lower than in *Drosophila* flies (Nei, 1975). Under the assumption that the enzymes studied represent a random sample of the genome, estimates of individual heterozygosity (H) in man are about 0.10; in mice approximately 0.09; and in *Drosophila* around 0.13. These studies also show that *M. domesticus* populations carried much of this genetic variation with them when they colonized the New World. Most of the alleles found in Danish, English, and Spanish *M. domesticus* have been found in North American populations. Danish *M. musculus* were about as variable as *M. domesticus*. Island populations of *M. domesticus* and *M. musculus* have slightly lower levels of heterozygosity than mainland populations in Europe (Hunt and Selander, 1973; Berry and Peters, 1977). However, it appears that the aboriginal species *M. spretus, M. abbotti,* and *M. hortulanus* are much less variable, with heterozygosity estimates in the range of 0–0.04 (Britton and Thaler, 1978; Sage, 1978; Sage and Marshall, in prep.).

The high levels of individual heterozygosity estimated from one-dimensional electrophoretic analysis of humans, mice, flies, and other organisms caused a revolution in the thinking of evolutionary biologists, and considerable debate was generated about the mechanisms that produce and maintain such variability. Evidence emerging from the first comparative two-dimensional electrophoretic studies suggests that the variability among the much larger array of proteins seen by this newer technique is less, by an order of magnitude, from the earlier estimates based on starch-gel electrophoresis of enzymatic proteins (Walton *et al.*, 1979; McConkey *et al.*, 1979; Racine and Langley, 1980b). However, it may be that this method of fractionating proteins is not very effective at separat-

ing allelic variants of proteins that differ only slightly in charge and hardly at all in molecular weight, and the earlier estimates of high genomic variability are correct. Or, it may be that a large majority of the proteins seen on these gels are of a functionally more constrained type (e.g. membrane-bound) and cannot support as much variation as the cytosol enzymes.

When used as markers for groups of related individuals, patterns of electrophoretic variation can demonstrate how house mouse populations are structured. Petras (1967a) and Selander (1970a) were able to show that mice living in barns could be organized into extremely small, stable breeding units. Thus, within the floor space of a single barn, analysis revealed geographical heterogeneity measured on the scale of a few square meters. Groups of animals sharing similar genotypes were assigned to restricted parts of the floor. Statistically significant differences in gene frequencies were found between adjacent barns on the same farm and between adjacent farms. But as Selander (1970a) points out, the interbarn, within-farm variance is 75% of the value of the between-farm variance. Thus much of the local variation can be found within populations living on a single farm.

On a continental scale in North America there may be some regional differentiation of mouse populations, but this is not very extreme, and seems to be the results of unique patterns of variation at each locus. Gradients of allelic change in North America follow an east–west direction at the *Es-3* locus, but a more north-south axis for the *Es-2* locus (Selander *et al.*, 1969b). Data available from Denmark (Selander *et al.*, 1969a), England (Berry and Peters, 1977), and southern France (Britton and Thaler, 1978) yield gene frequencies in European populations of *M. domesticus* on a north–south gradient. Information for a comparable series of north–south localities in the United States are available: Minnesota–Wisconsin, Illinois, Ohio, and Florida (Selander *et al.*, 1969b). At the β-hemoglobin locus, there is no discernible cline in Europe, but an increase in the Hbb^d allele from Minnesota to Florida. The *Es*-3, *b* allele increases in frequency from north to south in Europe, but shows a change in the opposite direction in the United States. The *Es*-5 locus demonstrates an increase in the *null, a* allele from Denmark to France, but in the United States this same allele is at a higher frequency in the extreme ranges than in the central populations. At none of these loci are the patterns similar between the two continents over wide latitudinal and temperature ranges.

R. J. Berry and colleagues have examined, in a series of studies, the changes in frequency of alleles in mouse populations from year-to-year, between younger and older mice, and between sexes. In many studies he has found significant shifts in allele and genotype frequencies. These changes have been attributed to the action of natural selection acting sometimes in directional manner and in other cases in a counter-directional, "endocyclic" manner. A long-term study of mice living on Skokholm Island showed regular seasonal changes in the frequencies of the *d* and *s* alleles of the hemoglobin locus, longer term changes in frequencies of a dipeptidase allele, and statistically significant departures in heterozygote frequencies at the *Hbb*, *Dip-1*, and *Es-2* loci (Berry and Murphy, 1970; Berry and Peters, 1977). On this island the frequency of the Hbb^s allele increased in 4 of 6 years between older (parental) animals and subsequent, younger progeny. This change was attributed to differential selection for alternate genotypes during the warmer, summer breeding season, and the cold winter season. The $Dip\text{-}1^b$ allele decreased from 0.92 to 0.66 frequency between 1967 and 1968, but by 1975 it had returned to near fixation. There were excess numbers of heterozygotes at the *Es-2* locus in males but not in females. But on two sub-Antarctic islands, the Hbb^s allele decreased in frequency between older and younger animals (Berry and Peters, 1975; Berry *et al.*, 1978). On a third south polar island, a marked and contrasting change in allele frequencies at the *Es-6* and *Got-2* loci was found in males versus females as they grew older (Berry *et al.*, 1979). These loci are on the same chromosome, and the data showed a statistically significant linkage disequilibrium between potential genotype combinations. The pattern of change is explained as due to stabilizing selection for alternate allelomorphs or the different chromosomes. In a study of mice from three tropical Pacific islands, no significant sex or age differences were found at ten polymorphic loci (Berry *et al.*, 1981). On these three islands, the Hbb^s allele decreased in frequency between older and younger mice in two cases. The lack of significant changes in allelic frequencies are attributed to relaxed selection pressures on mice living in warm climates, compared with the animals living on cold temperate islands.

As examples of the role of natural selection in determining gentoype frequencies, these results are based only on inferred causality. *In vivo* experiments with the various hemoglobin alleles have not been attempted. On a larger scale, there seems to be no consistent trend for altered hemoglobin frequencies in older–younger or summer–winter populations of mice. In seven different barns that were sampled during warm and cold seasons, Selander *et al.* (1969b) observed three cases where the Hbb^s allele increased between older (winter–early spring) and younger (summer) mice. Thus in the 18 comparisons discussed here of older mice and their younger progeny, the hemoglobin *s* allele has increased in frequency in only one-half of the cases. Invocation of the operation of natural selection to produce departures from Hardy–Weinberg expectations of genotype frequencies is dangerous. At the *Es-2* locus the presence of the *null, a* allele in the species makes it extremely difficult to be sure that accurate genotype determinations have been scored from the gels, and, indeed, the observed extreme excesses reported for the 1967–68 Skokholm samples could not be reconfirmed (R. J. Berry, personal communication). A

similar difficulty in unambiguously classifying the diffuse banded hemoglobin phenotypes has existed until the recently described technique of Whitney (1978) provided a way to produce distinctive banding patterns for all three of the common genotypes. Even a slight bias in scoring ambiguous cases will produce significant genotype departures without affecting the estimations of allele frequencies. In addition to the technical difficulties in scoring some phenotypes, there is the intrinsic effect of social structuring that may lead to radical departures from the expected binomial distribution of genotypes of the mouse populations. Selander (1970a) showed that at the *Es-3* and *Hbb* loci the departure of heterozygote frequencies from the expected values tended to be positive in small demes and negative in large populations. Kirby (1975) describes the demographic mechanisms by which such departures may arise based on chance factors, relating to gene frequency differences between the sexes in the mating generation and the random sampling of genotypes in the present generation.

Proteins have been used to identify taxonomic units in the house mouse group since the earliest applications of electrophoretic techniques. Selander and Yang (1970) concluded from their continent-wide survey of North American populations of house mice that two supposed subspecies (*domesticus* and *brevirostris*) could not be distinguished based on protein differences. In Europe, Selander and his group (Selander *et al.*, 1969a; Hunt and Selander, 1973) studied a zone of contact between the two species *M. musculus* and *M. domesticus* (called "semispecies" by these authors). That important study revealed many interesting things about the structure and dynamics of hybrid zones. They were able to show that the contact zone, running across the central part of the Jutland peninsula in Denmark, had remained stable for more than 20 years, and it was probably as old as the earliest farming cultures to occupy the region 5000 years earlier. The hybrid zone forms a band as narrow as 20 km wide, and free interbreeding between the forms takes place in this region. They observed that the zone was asymmetric: there was extensive introgression of *M. domesticus* alleles into *M. musculus* populations, but the reverse condition did not occur. This may be related to the social dominance of *M. domesticus* over *M. musculus* (Thuesen, 1977). They also reported the presence of alleles in very low frequencies at the *Es-2* and *Es-3* loci, but only in populations in the hybrid zone. This rare-allele phenomenon has now been reported in hybrid zones of a number of different types of animals (Sage and Selander, 1979), and may be a regular source of additional variability to such interacting species.

Schwarz and Schwarz (1943) described the presence of two sympatric subspecies (in their taxonomic scheme) that differed in morphology and ecology in southern Europe. This situation was studied in France (Britton *et al.*, 1976; Britton and Thaler, 1978) and in Spain (Sage, 1978). The free-living *M. spretus* and the commensal *M. domesticus* differed at many protein loci, showed no signs of natural hybridization, and were clearly different species. Despite the fact that they occur together naturally without mating, they will produce viable, but partially sterile, hybrids in the laboratory (Bonhomme *et al.*, 1978b, 1979). These same authors (Britton and Thaler, 1978; Sage, 1978) also point out that in western Europe there are no reliable protein differences distinguishing the more northerly subspecies *M. d. domesticus* from the southern *M. d. brevirostris* in their native range. The use of proteins to distinguish among the many described forms belonging to the house mouse complex has continued (Bonhomme *et al.*, 1978a; Minezawa *et al.*, 1979; Sage and Marshall, in prep.; and Fig. 1).

Other studies have looked for electrophoretic genetic variation at particular loci in wild-caught mice and tested for affects of insecticides on enzyme variation. Nielsen and Sick (1975) described the variation seen at two closely linked amylase loci in *M. musculus* and *M. domesticus* from Denmark, other parts of Europe, and North and South America. English *M. domesticus* with a variant allele at the glucosephosphate isomerase (*Gpi*) locus show reduced erythrocytic activity—similar to the pathological condition of humans suffering from GPI deficiency disease (Padua *et al.*, 1978). Peters and Nash (1976, 1977) searched for variation at the *Es-10* and *Es-11* loci in English *M. domesticus*. Variation at the *Ldh-A* and *Ldh-B* loci were reported in Spanish *M. spretus* and Hungarian *M. musculus* by Britton-Davidian *et al.* (1978). Examination of noninbred lines of Japanese *M. molossinus* and Thai *M. castaneus* showed variants for a pancreatic proteinase (Watanabe and Tomita, 1974) and the soluble form of glutamic–pyruvic transaminase (Eicher and Womack, 1977). A correlation between certain morphological and physiological traits and the biochemical genotypes of Skokholm Island *M. domesticus* was found using multivariate analysis techniques (Bellamy *et al.*, 1973).

Immunoglobin genes of wild mice were studied by Lieberman and Potter (1966, 1969). They found that five of the six known heavy-chain determinants of inbred strains were present in *M. domesticus* from North America. The determinant missing in wild North American mice is the one found in the C7BL strains. They later studied wild-caught *M. molossinus* from Japan and found that 9 of 10 specimens had this missing haplotype, providing support for the theory that this inbred strain contains genes from this wild species (Sage and Marshall, in prep.). Intra- and interspecific variation in murine complement protein, C-3, was reported by Natsuume-Sakai *et al.* (1979) in *M. d. praetextus* (Afghanistan, Pakistan), *M. castaneus* (Philippines), and *M. molossinus* (Japan).

An experiment to test the effects of the insecticide carbaryl (SEVIN) on wild mice showed no significant changes in frequency of alleles between the controls and the test populations at the *Es-2* and *Es-5* loci (Graf *et al.*, 1976).

E. Cytogenetic Variability

Only in the last decade has the great cytogenetic variability of wild house mice become apparent. Formerly, the mouse karyotype was believed to be composed of 20 pairs of one-armed (acrocentric) chromosomes that varied only slightly in relative size. Makino (1941) had shown slight differences in relative sizes among these acrocentric chromosomes in the laboratory *M. domesticus* (''albino''), wild *M. molossinus,* and *M. caroli.* I have looked at the gross karyotypes of *M. abbotti* (Yugoslavia), *M. hortulanus* (Yugoslavia), and *M. spretus* (Spain) and found them to be composed of 20 pairs of acrocentric chromosomes. Thus, the primitive karyotype of this complex is $2n = 40$ acrocentric chromosomes.

Newer cytological techniques and more field studies have exploded the traditional view, and we now know that there is a vast amount of cytogenetic variability in house mice. With the improved staining techniques now available, it has become possible to do fine structure studies and locate regions of different types of DNA. Quinicrine (Q), giemsa (G) banding, and nucleolus organizer staining now permit the unequivocal identification of each of the twenty pairs of mouse chromosomes (cf. Hsu *et al.,* 1978; Winking *et al.,* 1980). Studies on the variation in these patterns in wild mice is only beginning.

There is appprently a great amount of intrapopulational as well as interspecific differences in the amounts of centromeric heterochromatin. In a study of five wild *M. musculus* (Czechoslovakia) and one *M. poschiavinus* (Switzerland), Forejt (1973) reported that the first five animals were heterozygous at a minimum of 3–5 different chromosome pairs, while the Swiss mouse was variable on only one chromosome. Incidental to a study of the karyotype of *M. molossinus,* Dev *et al.* (1975) noted that different laboratory lines of this species were variable in their amounts of centromeric heterochromatin, and Ikeuchi (1978) reports on natural variation in the material on chromosome 18 in wild specimens from Japan. By making appropriate crosses, Dev *et al.* (1975) found that variation in amounts of this material was inherited in a simple Mendelian fashion.

Based on one study (Searle *et al.,* 1970) it appears that feral *M. domesticus* have fewer chiasmata per chromosome pair and are more resistant to ionizing radiation than laboratory mice. After conducting hybridization studies with *M. molossinus* and C57BL/6 inbred mice, Roderick (1971) concluded that these forms differed from one another by two or three paracentric inversions.

But perhaps the most exciting development in wild mouse biology of the last decade has been the discovery of many populations that carry bi-armed (metacentric) chromosomes produced through the fusion of two acrocentric chromosomes. Following the first reports (Gropp *et al.,* 1969, 1970) of the presence of seven pairs of metacentric chromosomes in Swiss alpine mice called *M. poschiavinus,* a large number of studies have revealed many other metacentric populations. Subsequent discoveries by Gropp, Capanna, and their colleagues (Gropp *et al.,* 1972; Capanna *et al.,* 1973, 1975, 1976, 1977a,b; Capanna and Valle, 1977; Capanna and Ricassi, 1978; and von Lehmann and Radbruch, 1977) have shown such populations to be widespread throughout Switzerland and Italy, and Dulić (1978) has reported a metacentric population in the coastal region of adjacent Yugoslavia. A. Gropp (personal communication) has found metacentric mice in Greece. All of these populations are derived from local, $2n = 40$ (no metacentrics) forms of *M. domesticus.* The recent report of two metacentric types in Indian populations, assignable by geography to *M. castaneus,* indicates that the phenomenon is more widespread (Chakrabarti and Chakrabarti, 1977). These discoveries in the house mouse complex will be of great importance for what they tell us about the general phenomenon of chromosomal evolution and speciation, both at the level of cytological processes and population dynamics. The great abundance of new chromosomal rearrangements present in these wild stocks promises to be an important resource for cytobiologists interested in altered chromosomal and genic relationships.

These European studies show that many of the samples are made up of populations with variable numbers of metacentric pairs (Fig. 2). In the best studied cases of heterozygous samples, the collections indicate that they come from narrow zones of hybridization between more extensive homozygous populations (Capanna *et al.,* 1977a; Capanna and Ricassi, 1978; Spirito *et al.,* 1980). Some localities with heterozygotes (e.g., Palermo, Lörrach, and Andalo) represent either pooled samples from a larger area or collections from single buildings. Further studies in these regions are expected to show nearby larger areas occupied by homozygous populations. It is evident from Fig. 2 that populations may have from one to a maximum of nine pairs of metacentrics. [The sex chromosomes are never involved in forming metacentrics, so the remaining nineteen pairs of autosomes may fuse to form a maximum of nine metacentric pairs + two unfused chromosomes]. Furthermore, the geographical distribution of these fusion populations is heterogeneous: Through the Rhine valley of the Swiss Alps, samples with only one metacentric pair are present, but both to the north and south there are higher numbered populations.

Although populations may have the same number of metacentric pairs (e.g., Orobie and Apennine CD each with 9), there are important differences in the composition of the metacentrics in animals from the two regions. Eighteen pairs of acrocentrics appear to fuse in a nearly random manner to produce metacentrics made up of different combinations of the acrocentric set. Thus between the two sets of metacentrics in the Orobie and Apennine CD populations, only one pair, formed by the fusion of the acrocentrics No. 10 and No. 12 (10·12), is similar in construction (Table III). All sixteen of

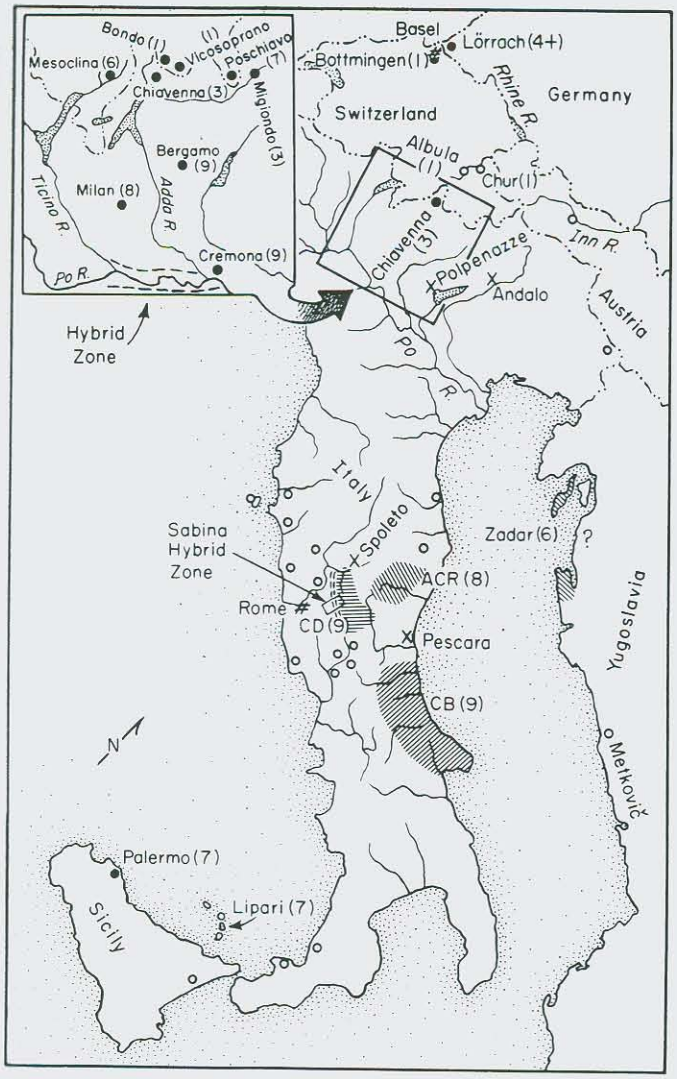


Fig. 2. Distribution of metacentric chromosome populations of house mice. Numbers in brackets indicate how many metacentric fusions are in the karyotype. Open circles indicate samples of mice showing no metacentric fusions.

the remaining metacentrics in these two populations are formed by differing combinations from among the remaining seventeen acrocentrics. Analyses of the fine structure of the fusion combinations has shown that some populations within large geographical areas share the same set of fused chromosomes, while other nearby samples may have a nearly completely different set. The three geographically contiguous Apennine populations, CD (Cittaducale), CB (Campobasso), and ACR (Ancarano) demonstrate these types of differences very clearly (Fig. 2, Table III). The CD and CB populations have only one identical metacentric (9·16), CB and ANC have two in common (8·14 and 10·12), and there are no identical fusion products shared between CD and ACR. This demonstrates the remarkable fact that most of these metacentrics have been produced independently in three neighboring regions.

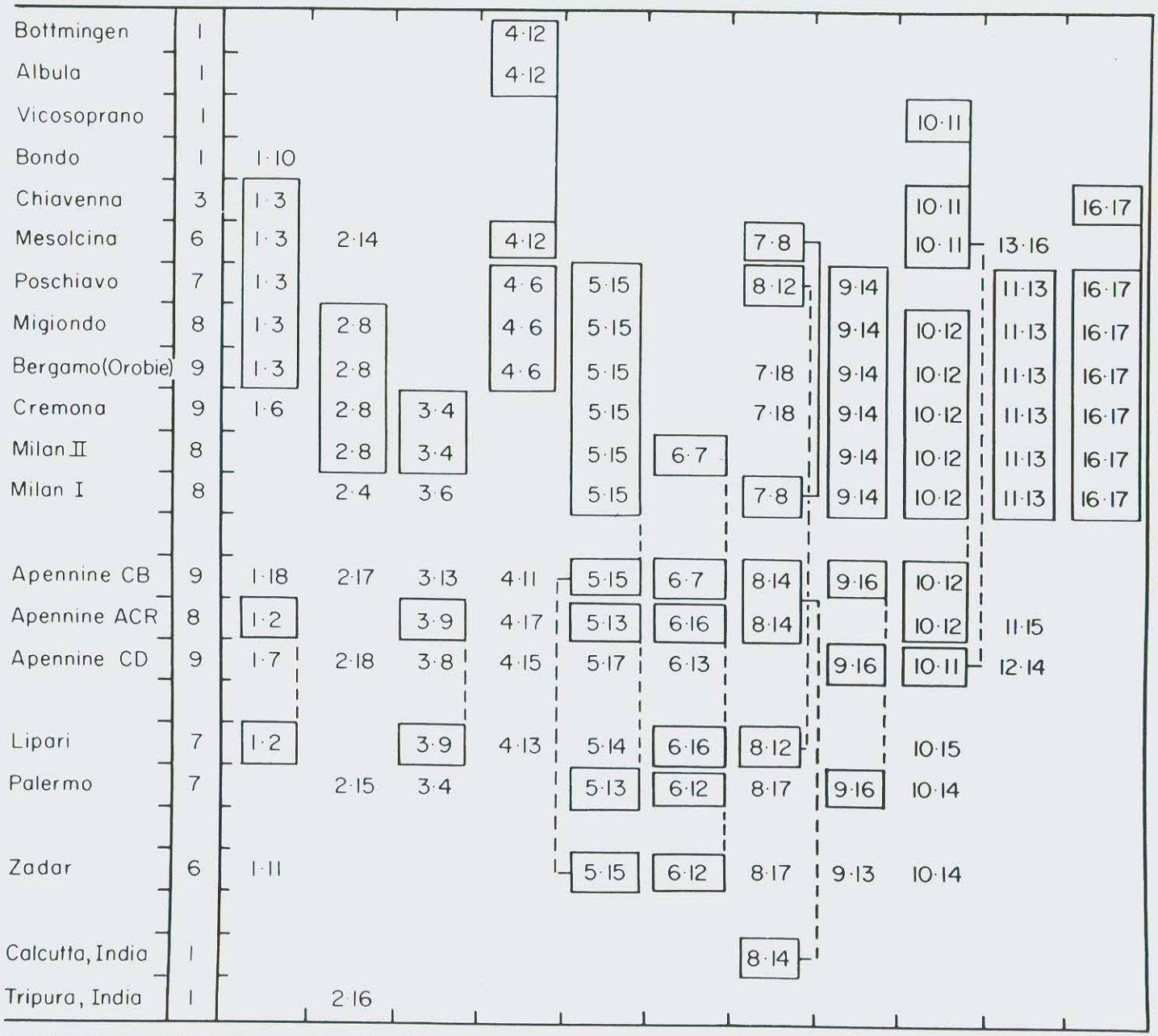
However, apparently not all systems are derived *de novo*. Some of the metacentrics may arise in populations ancestral to ones that are presently slightly different from one another. A particularly convincing case for a common ancestral state of some populations is seen in the southern alpen region. The two highly derived groups of the Orobie and Poschiavo systems have 12 identical metacentrics in a total of 16 (Table III). They share six pairs of metacentrics: 1·3, 4·6, 5·15, 9·14, 11·13, and 16·17. Because of their geographical contiguity, it seems most probable that they shared a common ancestor up to the six metacentric stage, before becoming separated and producing two more different combinations in the Orobie system and one more in the Poschiavo valley.

An additional feature of the geographical distribution of these different populations is worth mentioning: the role that partial physical barriers seem to play in limiting the ranges of some of these metacentric complexes. In the Apennine region, the CD populations are partially enclosed by the barriers of mountain massifs on the north and south (Capanna *et al.*, 1977a). The Milan and Orobie systems are separated from one another by the Adda river, and the Milan system is separated from nonmetacentric populations in the south by the Po river (Capanna and Valle, 1977). A similar situation may be operating in the region around Basel (Fig. 2). Here the populations at Bottmingen, on the south side of the Rhine river, have one metacentric while less than 10 km north at Lörrach (Germany), on the opposite side of the river, the population contains a minimum of four different metacentrics (Gropp *et al.*, 1972). Rivers acting as boundaries to the ranges of chromosomally distinctive forms of rodents is also clearly seen in the pocket mouse, *Perognathus goldmani* (Patton, 1969), and such partial barriers to population interchange may be an essential feature for this type of chromosomal differentiation in otherwise similar organisms.

The presumptive common origin of some metacentrics in different populations leads to a discussion of how these complex karyotypes arise. It should be stated that our present knowledge of these systems is still in a very primitive state; ongoing field and laboratory studies of more samples may provide a very different interpretation of the processes of Robertsonian evolution in these mice. Nevertheless Capanna *et al.* (1977a) and White (1978a) have speculated on the manner in which such fusion populations are produced. One model invokes a single mutational event producing a mouse heterozygous for all of the metacentrics that will subsequently be established in the populations through backcrossing and close inbreeding in the founding deme. The alternate proposal is that the present multimetacentric populations have been established through repeated cycles of single metacentric mutations, followed by fixation and geographical expansion. The

Table III

Distribution of Metacentric Chromosomes in House Mouse Populations[a]



[a] Data from Gropp *et al.* (1972), Capanna *et al.* (1976, 1977a), von Lehmann and Radbruch (1977), Gropp and Winking (1981), and Chakrabarti and Chakrabarti (1977).

first model (SSM—single simultaneous mutation) receives little support based on laboratory experiments, where all mutations have produced only one fusion product at a time. There is also no theory for such total control mechanisms in operation in the meiotic cell [but see Holmquist and Dancis (1979) for a cellular mechanism for producing multimetacentrics at one time], and finally, because the expected reduction in fertility of the multiply heterozygous founder animal would predict a very low probability of producing viable backcross progeny. A model based on repeated, single mutational events (MSM-multiple single mutations) is considered more likely by both Capanna *et al.* (1977a) and White (1978a). Laboratory and field evidence is supportive of this theory.

The occurrence of the same metacentric combinations in adjacent populations is consistent with a repeated series of single mutations followed by spreading, but with occasional interruption and separation of populations during later stages of the cycle. Under the SSM model, the metacentrics shared by populations would be ascribable to convergent mutations, whereas under the MSM model most of these would be expected to be derived from a common ancestor. This latter expectation is based on the low, chance probability of the same two chromosomes fusing together more than once. A total of 171 unique chromosomal combinations (19X18/2) are equally possible. The probability of the same combination occurring twice by chance is low ($p = 3 \times 10^{-5}$). There are 108 metacentrics chromosomes known in these European samples (Table II), of which 48 are different. While it seems impossible that all 60 of the duplicates are independent mutations and some must owe their origins to commonality, it may be that some of them do indeed represent convergence. Based on geographical and genetical relationships, the apparently identical fusion (8·14) in the Apennine CV and the Calcutta, India sample must represent such a convergence. Within the European mice, it really is not clear whether the apparently large geographical separation of some metacentrics [e.g., the 1·2 metacentric shared between the central (ACR) and southern Italian (Lipari) populations, or the 5·15 metacentric shared by the Orobie and Apennine CB units] represents ancestral relationships or convergence.

Unless a nonrandom preference of association between acrocentrics is shown, then the low probabilities for such duplicate mutations argues in favor of identity by common descent. Analysis of populations in intervening areas will clear up some of these questions. Under the prediction of a common ancestor and single mutation events, it is expected that these particular metacentrics will occur in these unstudied regions. The examination of the allelic identity of genes found on the duplicated metacentrics might also provide evidence for or against the idea of common descent.

The only indication that there is a nonrandom association between different acrocentrics is that the smallest autosomes pair (No. 19) is not represented in any metacentric combination in Table 2. With a random chance of 1/19 of any acrocentric being included in a metacentric combination and a minimum number of 48 different mutations having occurred in the European mice, every autosome should be represented 2–3 times among the identified metacentrics. What is most puzzling is that among the 10 independently derived metacentrics in laboratory stocks (Gropp and Winking, 1981), three of them (30%) involve chromosome 19! Although White *et al.* (1978) found that chromosome 19 did not produce disproportionate numbers of aneuploid gametes when it was studied in a laboratory-derived metacentric, it may be that some acrocentric combinations produce such detrimental effects that they are eliminated by natural selection in the wild stocks. Both Cattanach and Moseley (1973), Gropp *et al.* (1974), and Gropp and Winking (1981) report that different metacentrics from *M. poschiavinus* produce varying amounts (4–26%) of abnormal meiotic figures due to nondisjunction in heterozygous animals. Such varying reductions in viability may be the reason that some acrocentric combinations do not become fixed in the presumably nonlethal, homozygous condition.

The origins of such chromosomally differentiated forms have been reviewed by White (1978b). In many papers he has argued that rapid differentiation of populations may occur through chromosomal rearrangements. The case of the European house mouse fits very well into the process that he calls *stasipatric speciation*. This involves a mutation to produce a chromosome rearrangement in a local population, followed by rapid fixation of the mutant and its range expansion at the expense of the surrounding, ancestral form. The observation of the repeated cycling of this sequence of events in derived populations has been called *karyotypic orthoselection* (White, 1978b). He offers the hypothesis that this buildup of homozygous rearrangements is favored by natural selection as a means of isolating a group due to increasing levels of hybrid inviability. One of the correlates of this manner of evolution is that the oldest mutations should be found in peripheral populations, whereas the most recent mutations are expected in more central regions of the distribution.

The house mouse data is consistent with this model of stasipatric evolution. In the alpine region, we find the single metacentric 4·12 at Rhine river localities, but on the southern border of the drainage system this metacentric is embedded in the multimetacentric populations in Val Mesoclina (Table III). Under the stasipatric model, the Mesoclina regions is the one from which the original mutant arose, and has subsequently spread down the Rhine valley to near Basel, where it now confronts another metacentric population on the north side of the river (Lörrach). Evidence in support of the unidirectional increase (orthoselection) in metacentrics is supported by the finding of many individual metacentrics shared among the alpine populations. This would be explainable on the basis of

repeated single mutation events becoming fixed and most frequently spreading into adjacent metacentric populations rather than into nonmetacentric animals.

It is apparent that this process may proceed at an extremely rapid rate. For the most part these metacentric mice are identical in external appearance with their nearby ancestors. The mice of the Poschiavo-Valtellina system (*M. poschiavinus*) are black in coloration rather than brown. This was the criterion on which the species was first described, although black coloration is known in other mouse populations. It should not be assumed that this melanic variant is a character without survival value. In this same region populations of the snake *Coluber viridiflavus* are also melanic, and it is probably not a coincidence that two different animal species should assume a similar coloration in the area. But in spite of this hint of local adaptation, it is apparent that all of this chromosomal evolution has proceeded during a very short period of time. The enzyme profile of *M. poschiavinus* shows that it has no alleles that were not found in *M. domesticus* populations from Europe and North Africa (Sage and Marshall, in prep.; Fig. 1), so there is no support of a sufficiently long period of time for new biochemical mutants to arise and become fixed in these isolated populations. Britton-Davidian *et al.* (1980) did not find signs of divergence of other metacentric populations from their all-acrocentric neighbors in an electrophoresis study, but observed a reduction in genic heterozygosity of the derived chromosomal forms. With analytical centrifuge techniques, Comings and Avelino (1972) found no evidence of a decrease in satellite DNA that would suggest the loss of centromeric material in *M. poschiavinus*. Using another approach, Redi *et al.* (1974) came to the same conclusion for the CD metacentric form. However, there does seem to be some divergence away from a constant amount of nuclear DNA content in *M. poschiavinus* (Romanini *et al.*, 1971), and this should be studied more carefully. Furthermore, the obligately commensal relationship of these mice with human dwellings implies that they did not arrive in the area prior to agricultural settlements (approximately 8000 years BP). The extremely rapid rate of chromosomal change dictated by these conclusions remains unexplained.

Whatever the mechanisms are that produce the mutations and drive them to fixation, it is clear that some of these populations have achieved an effective reproductive isolation from others. Genetic isolation becomes increasingly great as more metacentrics are fixed in a population due to decreased fertility. Crosses between different multimetacentric populations are sterile. In the zones of contact between such populations, there will no longer be gene flow due to introgression; there will only be competitive interactions of the type observed between ecologically similar species. Narrow hybrid zones do exist at the boundaries between metacentric and nonmetacentric populations. These are documented along the Po river at the southern edge of the range of the Milan population (Capanna and Valle, 1977) and in the Sabine hills at the western edge of the range of the CD population (Capanna *et al.*, 1977a; Spirito *et al.*, 1980). Given that metacentric populations must have displaced ancestral, nonmetacentrics in their present ranges, it seems reasonable to conclude that these hybrid zones are currently unstable and are moving into the range of the nonmetacentric mice. I would think that only during the earliest stages of this contact between the nonmetacentrics and the derived forms, when only one or two metacentrics are involved, would viable hybrids be produced in great enough numbers to permit gene flow into the metacentric population. Once many fusions were present in the chromosomally altered population isolation would be effectively complete between the two forms, even though a few hybrids were still being produced.

The study of the metacentric mouse populations is not completed, and many questions remain unanswered. Yet even at this date, this case has provided important data on some of the things that are going on during a bout of chromosomal speciation. The mouse data shows that reduced fertility of heterozygotes does occur due to meiotic problems, and reproductive isolation may occur without other forms of differentiation. The banding data shows that different arms may be fused to form metacentrics and that the arm composition of the metacentrics is largely random. The common distribution of low and high numbers of metacentrics in peripheral versus central populations is supportive of the stasipatric speciation model. Important questions that remain unanswered concern the production of metacentrics, the dynamics of their fixation and geographic spread, and the re-creation of the evolutionary sequence in the European populations. We have little understanding of how so many mutants can spread so far so quickly. For example, in the CB populations a minimum of nine mutations were sequentially produced and spread over an area of approximately 7500 km^2 in less than 8000 years. What selective advantage does the more derived chromosomal form have over the primitive type? What causes so many of these mutations? Meiotic drive, assortative mating, and viral infections have been suggested (Capanna *et al.*, 1977a; White, 1978b). Gropp and Winking (1981) comment that many of the recently reported new metacentrics in laboratory mice have appeared in stocks already carrying one of the *M. poschiavinus* chromosomes. This suggests that an intracellular agent, rather than an environmental factor, is responsible for these mutations. The continued sampling of populations in the intervening areas between the southern islands, central Italy, and the alpine systems will reveal how much of the chromosome similarity between these adjacent regions is due to common ancestors or convergent mutation. Evidence for the latter finding would predict that certain combinations of acrocentrics are favored over others, and it might provide clues as to what makes the metacentric

condition so favored. The Lörrach sample suggests that this process is occurring on the northern side of the Alps as well.

F. The *T* locus

A particularly interesting form of genetic variation in wild mice is found at the *T* locus. This gene complex has figured importantly in the study of wild mice because of the intriguing fact that, although the variant alleles may be lethal in the homozygous condition, they are widespread in mouse populations. Persistence of these seemingly deleterious genes has made them the object of study by laboratory, field, and mathematical population biologists. Recent review articles on the *t* alleles include those by Sherman and Wudl (1977), Bennett (1978), and Lacy (1978).

The salient feature of *t* alleles is that they are a series of variably deleterious mutants that are passed on to progeny of heterozygous males at a much higher frequency than expected by chance. They also cause a repression in crossing over in this region of chromosome 17. The increased transmission rate of a *t* versus + (wild type) allele can reach unity in some cases. This enhancement is assumed to be the factor that keeps such a deleterious gene in the populations, and the dynamics of this interaction between beneficial and detrimental effects has produced many studies describing the behavior of *t* alleles.

The *t* alleles seem to be widespread in house mice. They have been reported in *M. molossinus* from Japan (Tutikawa, 1955). *M. musculus* from Russia and northern Europe (Dunn *et al.*, 1973), and in *M. domesticus* from Europe and North America (Lewontin and Dunn, 1960; Dunn *et al.*, 1973). In Europe, it was shown that some of the same alleles are found in both *M. musculus* and *M. domesticus* (Dunn *et al.*, 1973), suggesting considerable antiquity for some of these mutants. It is also clear that the colonizing mice of the New World carried many of the variants with them from Europe. Although the genes are widespread in mouse populations and may reach appreciable frequencies (0.15–0.20), they were not found in a search among field-dwelling, feral mice in California (Myers, 1973).

Both deterministic and stochastic types of mathematical models have been used to predict the distribution of *t* alleles in mouse populations (Prout, 1953; Bruck, 1957; Lewontin and Dunn, 1960; Lewontin, 1962; 1968; Young, 1967; Levin *et al.*, 1969). These models dealt with the consequences of varying parameter values for the fitness of different genotypes, the degree of inbreeding in mouse populations, the size of breeding units, and rates of migration. The general conclusion is that, if mouse breeding units are small, the effects of selection on the alleles would be minimized and chance effects would prevail in determining the overall frequency of *t* alleles in mouse populations.

Detailed field studies of infected, barn populations of mice were done by Anderson *et al.* (1964) and Petras (1967b) to determine what the dynamics of the alleles are in the natural state and what the actual values might be for the parameters used in the mathematical models. Petras (1967a) used data on an enzyme polymorphism to estimate the degree of inbreeding in the social units. Both workers found significant variation in frequencies of *t* alleles between barns or ricks, and there was variation between years. Various *t* alleles were found to coexist in the same deme. They found small breeding units that persisted through time, and Anderson *et al.* (1964) noted very low levels of successful migration between breeding units.

Experimental manipulations of mouse populations using *t* alleles have been attempted to study breeding structure and population regulation. A lethal *t* gene was introduced into a population on Great Gull Island in New York during 1956 and 1957. Although individual mice can theoretically traverse the entire length of this small island, the allele spread very slowly during the following 10 years (Bennett *et al.*, 1967). The slow spread of the gene was considered as proof of the very stable and closed breeding structure of mouse demes on the island (Anderson *et al.*, 1964). However, 15 years after introduction the lethal allele appeared to have become extinct on the island (Bennett, 1978). Reasoning that lethal or sterility genes might be used in controlling the growth of mouse populations, Pennycuik *et al.* (1978) introduced *t* alleles into a large enclosed population and studied the effects during a 4-year period. They found no observable regression of population growth or size after the successful introduction of the lethal allele. They also found that the allele declined to apparent extinction within 2 years after its first introduction.

While studies of *t* alleles have been the stimulus leading to our better understanding of the population structure of house mice, our understanding of the dynamics of these genes in populations has not been so great. Lacy (1978) questioned whether they have a direct adaptive function for the individual, or whether they serve to enhance the survival of larger breeding groups. But recent studies (reviewed in Sherman and Wudl, 1977; Nadijcka and Hillman, 1980) provide strong support for the idea that the superior metabolism of *t*-bearing sperm leads to their higher rate of fertilization success, rather than their having a negative effect on the non-*t*-bearing gametes. This system would then become a simple case of gametic selection at the spermatozoan level. Absence or loss of *t* alleles in outdoor populations led Myers (1973) to suggest that they are at a disadvantage in this environment compared to a commensal habitat. More studies of wild populations are needed to firmly establish that *t* alleles are rare in the out-of-doors. Electrophoretic techniques for identifying *t*-bearing animals are now available (Silver *et al.*, 1979), and this will greatly simplify the amount of work needed to survey wild populations. Their association with the histocom-

patibility complex (*H-2*) is discussed in the following section.

Forejt and Ivanyi (1975) described a gene causing male sterility in mice that is located within the region of the T complex. This gene was first discovered as a result of mating wild *M. musculus* from Czechslovakia and Denmark with the inbred C57BL/10 strain. Such a sterility factor may be one cause for the narrow zone of hybridization between *M. domesticus* and *M. musculus* in Denmark. How widespread is its occurrence in wild *M. domesticus* is not yet known.

G. Histocompatibility Complex

The structure and function of the *H-2* complex has been reviewed by Klein (1975) also, see Chapter 7, this volume, David (1977), and Snell (1979). The importance of this series of 9+ loci in the major histocompatibility system of the mouse cannot be overestimated. These genes function in the recognition and rejection of foreign antigens such as virus particles and in the mediation of cooperative interactions between different types of lymphocyte cells in the antibody response. It may even be involved in nonrandom mating preferences between mice of the same haplotype (Yamazaki *et al.*, 1976). Significantly perhaps, the *H-2* complex is on the same chromosome with the *T* locus complex just described, and the crossover suppression effect of that complex encompasses the *H-2* region as well.

Early work using inbred strains of mice revealed a variety of different graft-rejection and cytotoxically-definable "alleles." At least 10 of these "alleles" were known in the inbred strains: a number of variants much higher than reported for other mouse loci. Further studies showed that the *H-2* "gene" was not one locus but a length of chromatin containing a duplicate series of *H-2* genes (*sensu strictu*) as well as an intervening region containing the *I* and *S* genes. The large number of variant chromosomes, now called *H-2* haplotypes, that were found in inbred strains presaged the discovery of an even larger series in wild mice. Studies of wild animals indicate that there is a huge amount of genetic variation in this chromosomal segment, rivaling that found in the comparable (homologous) major histocompatibility system of humans, the HLA complex. Although comparative studies of wild mice are still few in number, they have answered some questions about the patterns of variability of these genes in mouse populations. They are sufficient to provide a preview of the huge amount of variability that must still be present in the wild, and they pose a series of interesting questions about the function and dynamics of these genes and the linked *T* locus complex in the natural world.

The *H-2* system has been studied in *M. molossinus* in Japan (Moriwaki *et al.*, 1979); *M. musculus* and *M. domesticus* in Europe (Mikova and Iványi, 1976; Iványi and de Greeve, 1978); *M. domesticus* in Chile (Pizarro *et al.*, 1977) and in the United States (Klein, 1970; Klein *et al.*, 1977, 1978). The early studies by Klein (1970) of feral mice in Michigan showed two things about the *H-2* system. Of 40 wild mice tested against 15 antisera derived from inbred strains, some animals (*null*) did not react with any of the test antigens, whereas some antigens were nearly ubiquitous in occurrence. The finding of *null* animals showed that the wild animals contained variants not represented in any of the inbred stocks, indicating more variability than was then detectable. Some antigens of inbred mice were absent from the wild mice suggesting that the founders of these stocks came from populations with different chromosome types than those present in the Michigan mice. The other thing shown by this data was that the groups of animals collected at four different localities differed from one another in the occurrence of the various antigens. This is corraborative evidence of the closed social structuring of mouse breeding units on a local scale. An additional 20 congenic, new *H-2* chromosomes were isolated from these Michigan mice. There are now 109 haplotypes known, including variants for gene products in the middle, *I* and *S* regions of the complex. At the two *H-2* loci proper, there are 69 alleles (37 at *H-2K* and 32 at *H-2D*). In a combinational fashion they provide a minimum of about 1200 unique chromosomal arrangements. Using the expanded array of *H-2* and *Ia* sera in their testing program, Duncan *et al.* (1979) studied 88 wild mice from Texas for their degree of heterozygosity. Their results indicated a minimal heterozygosity level for the four loci studied of 96%. At the individual locus, percent heterozygosity was 100 (*H-2K* and *H-2D*) (*Ia-1*) and 47 (*Ia-5*). This is to be compared with the average heterozygosity level at enzyme loci of about 9%. Their data on frequencies of the alleles at the three most polymorphic loci is on the order of 2%, with an estimate of 100 alleles present at each locus. Essentially there are no homozygous animals in the population. The meaning of this high level of heterozygosity in evolutionary terms begs an answer. More than a decade ago, Snell (1968) proposed a number of hypotheses about the adaptive advantage for the high levels of variation known at that time. The arguments center around a strategy of variability to protect the mouse from the wide array of chemical antigens produced by microorganisms and viruses in their efforts to penetrate cell membranes. In this onslaught, there is expected to be an evolutionary race between the pathogens and the hosts, in which the attackers try to mimic the protein markers of the hosts in order to pass unhampered into the cells. A large variety of "self"-recognizing proteins in the host cells would make it improbable that the pathogens could evolve a protein combination that would permit an easy, or a biochemically cheap, entry into the cells. In this general context, Snell (1968) suggested that the *T*

locus complex might have a functional relationship to the *H-2* complex. Because *t* alleles are lethal in the homozygous state they do serve as a mechanism to insure some outbreeding in an organism which hae a tendency to produce inbred demes under certain environmental conditions. This action of the *t* alleles would ensure some *H-2* heterozygosity. Such an idea of a supergene complex is appealing. Because so little experimental effort has been made to determine what the selective advantages of heterozygosity versus homozygosity are at the *H-2* or the *T* complex, trying to combine the two systems into one evolutionary unit is still premature.

Aside from heterozygosity analyses, studies of the *H-2* complex have shown that *M. molossinus* differs from *M. domesticus* in frequencies of the various haplotypes (Moriwaki *et al.*, 1979). A finding of evolutionary interest is that the complementation groups of the *t* allele series have the same *H-2* haplotypes (Hammerberg *et al.*, 1976). Thus *Mus domesticus* with the t^{w1} complementation group, collected in Denmark, New York, and California, all have the same $H\text{-}2^{tw1}$ haplotype. Such similarities of chromosomes taken over large geographical ranges suggests how resistant these chromosomal segments are to recombination. The adaptive advantage of specific *H-2* variants has not been demonstrated in wild mice. Perhaps some of the unique haplotypes of *M. molossinus* control the AKR proviral genome of MuLV which occurs in this species (Sec. II,D, 3).

H. Drug Resistance

Genetic resistance to the rodenticide Warfarin has been studied by MacSwiney and Wallace (1978) in English populations of *M. domesticus*. Populations from three localities were found to have a major Warfarin resistance gene (*War*) located on chromosome 7. This major gene shows penetrance effects of sex and age modifers. *War* maps to approximately the same position on a linkage group as the Warfarin resistance gene (Rw^2) of the rat, *R. norvegicus*.

IV. PHYSIOLOGY

In its spread, first across Eurasia, then virtually around the world, *M. domesticus* has successfully occupied and succeeded in a variety of habitats ranging from warm to cold and wet to dry. Yet, how the mice meet these contrasting environmental challenges at the physiological level is not well-studied. I found no information on genetically based variation in characters such as basal metabolic rates or temperature preferences of wild mice. Available studies have concentrated on the adaptations to living in the cold, and to the capabilities of mice to exist without free water. Recent field studies—now corroborated in laboratory mice—show that cold-stressed animals have the capabilities of undergoing torpor.

A. Cold Temperature Adaptation

In their studies of Skokholm mice, Berry and Jakobson (1975) have stressed how critical cold temperatures are to the survival of mice. After an extremely cold winter, the spring sample may contain only 10% of the population from the preceding autumn. Barnett has explored the affects of cold (−3°C) temperatures on laboratory and wild mice in a series of studies (reviewed in Barnett, 1965, 1973; Barnett *et al.*, 1975, 1978). He showed that the most important short-term, physiological, and behavioral response of cold-stressed mice is to increase their heat-producing metabolism to 4 times the level of control mice, and they begin to make nests of better structural quality. Development and reproduction are strongly affected by the cold: age at maturity is retarded by about one week, and the estrous cycle slows from an average of 1/4.8–8.5 days. Nestling mice grow more slowly than controls. He speculates that a lactating female may be eating the maximal amount of food that can be digested to keep her own heat production high as well as provide nourishment to the young. Interestingly, Fertig and Edmonds (1969) found that mouse milk was similar to that of marine mammals in having a very high fat–low water content, a favorable condition in the cold. Strecker (1955) noted a correlation between increased food consumption and cold temperatures in a marked Wisconsin population. And when acclimated and nonacclimated wild mice were tested at cold temperatures, the acclimated animals spent more time away from the nest in exploratory behavior (Barnett *et al.*, 1978). Challenged by the cold, nonacclimated animals apparently had to direct their available energies into heat production at the expense of activity. When wild stocks were raised in the cold environments for many generations there were genetically based changes in the reproductive behavior (Barnett *et al.*, 1975) (see Sec. VI,A).

Field studies of the hematological characteristics of wild *M. domesticus* are consistent with the idea that in cold weather the animals greatly increase their metabolic rates. MacLean and Lee (1973) studied the hematological parameters of a barn population in Australia during the summer and winter. They found that all of the standard characters, such as hemoglobin concentration and blood volume, showed a significant increase during the winter. They related this to demands by the tissues for more oxygen to maintain increased levels of heat production. Berry and Jakobson (1975) reported the same trends in samples of mice from England. Winter survivorship was correlated with several morphological and hematological measures in 2 years (Jakobson, 1978). But since multiple regression analyses showed that different parameters were important in

the 2 years, it was concluded that single physiological characteristics did not have a consistent influence on the survival of the individual mouse. Variation in hematocrit levels is known to be under the control of several loci (Schlager and Weibust, 1976).

Solomonov *et al.* (1971) claimed that the preferred temperature of *M. musculus* from near Yakutsk in northern Soviet Union was lower than for this species to the southwest. However it is likely that they were comparing their results with data obtained on *M. hortulanus* or *M. abbotti*.

Recently Morton (1978) made the surprising finding of torpid wild *M. domesticus* in Australia. These animals had body temperatures ranging from 18–21°C (the normal body temperature of mice is 36°–37°C). These animals could not stand upright, but became active within 30 min of disturbance. Some of these nests were being shared by groups of torpid *Mus* and specimens of the fat-tailed marsupial mouse, *Sminthopsis crassicaudata*. They regard this as a case of "thermoregulatory mutualism." In fact, torpor has been described before in wild mice: in *M. musculus* (?) on the Faroe islands (Degerbøl, 1942) and laboratory stocks of feral *M. domesticus* from California (Fertig and Edmonds, 1969). Hudson and Scott (1979) have now studied the physiology of this behavior in domesticated mice. The limited amount of field data are consistent with their findings, and they provide more quantitative measures of the various physiological and behavioral events associated with torpor. How extensive a role this behavior may have for mice in resisting cold stress is not known. The aboriginal species should be tested for any enhanced capabilities in this regard.

B. Water Balance

Mus domesticus may be stressed by lack of water, particularly, in the natural desert environment and in stored-food habitats. If, as seems reasonable from the native distribution of *M. domesticus*, this species evolved in the more arid parts of Eurasia, then it is expected that it will be able to handle low-water stresses. Koford (1968), impressed with finding house mice in the very arid Sechura desert of Peru, tested wild mice (from California) for their response to a water-free diet of seeds. The animals quickly lost about 10% of their body weight, but gained this back within a few days and survived until the end of the experiment. A more rigorous and extensive experiment was performed on wild mice by Haines and Schmidt-Nielsen (1967) and Haines *et al.* (1973). Mice were tested on a seed diet in a controlled-humidity chamber (Relative Humidity (RH) = 80, 60, 40, 30%). Nonacclimated mice survived at 60% RH, but all died at 40%, whereas acclimated animals could survive at 40% but died at 30% RH. By way of contrast, they noted that the desert kangaroo rat (*Dipodomys merriami*) does well at 24% RH, whereas the Norway rat (*R. norvegicus*) starts losing weight at 95% RH. Fertig and Edmonds (1969) found that water-stressed wild mice could lose up to 40% of their weight and then regain it within 40 hr. They and Haines and Schmidt-Nielsen (1967) found that the urine is highly concentrated and that mice could drink sea-water and survive. Mice lose little water through pulmonary evaporation, and their feces have a very low water content (Fertig and Edmonds, 1969). The characteristics of the urine from 15 mice collected in a salt marsh did not indicate extreme conditions, and Greene and Fertig (1972) conclude that the mice obtained sufficient fresh water from animal matter and dew to go unstressed by this salty environment. In all of these ways *M. domesticus* seems to be physiologically well-adapted to a desert environment, and preadapted to the sometimes, very arid, commensal habitats.

V. BEHAVIOR

The subject of behavior can be considered as including all of the activities of the whole organism, and under that broad definition much of this review could be considered a study of wild mouse behavior. Most of this information has been partitioned by other titles, and what remains here is a summary of activities related to the domestication process of the common laboratory strains, daily maintenance, and, the dispersion behavior that relates the animal to its place in the environment and to other members of the same population.

A. Domestication and Inbreeding

The contrast in the behavior of a wild mouse and a domesticated, fancy or laboratory animal is obvious to any one familiar with both types. What process led to the docile behavior of the domestic form has been of some interest and has led a number of workers to try to quantify and determine the genetic basis for this condition. Dawson (1932) showed that wild *M. domesticus* escaped from a runway in a much shorter time than did domesticated fancy mice and discovered, by appropriate laboratory crosses, that the difference was heritable. Rapid running behavior appeared to behave as a dominant character in the wild stock. Smith (1972, 1978a,b) tried to quantify the differences between random-bred strains of wild mice and domesticated inbreds. The most notable differences were in the high levels of wheel running activity of the wild mice, the almost complete lack of jumping behavior by the inbreds, and an open-field "freezing" stance in wild animals. After brother–sister mating for 10 generations, Connor (1975) found a strongly reduced level of intermale aggression and a partially

reduced resistance to recapture. For seven other behavioral traits, there were no differences after inbreeding. Smith and Connor (1978) concluded from their studies of random-bred and inbred lines of wild-caught mice that laboratory breeding per se did not result in a more "domesticated" state of behavior. Variation in behavior of the wild stocks of *M. domesticus* was used to test for the heritability of these traits; both Smith (1978b) and Ebert and Hyde (1976) were able to produce lines of mice having statistically significant differences within three to four generations after selection for high and low levels of shuttle avoidance and agonistic behavior. Lynch (1977) observed little effect on four morphological and behavioral traits after five generations of inbreeding of wild mice. But Connor and Bellucci (1979) observed a drastic decline in the fertility of wild mouse stocks only in the last stages of a 20-generation inbreeding program. Random-bred animals from the same original stock did not show this loss of reproductive performance through the same time period.

In an experiment designed to test what effects domestication had on the behavior of the laboratory mouse, Reimov *et al.* (1968) released white mice (*M. domesticus*) and locally caught wild mice in an attic in Poland. The results of the experiment showed differences between the two groups in their degree of trappability, times of activity, and rates of disappearance from the study area. Furthermore, by recapturing and isolating the female laboratory mice after 30 days of freedom, they showed that 89% of the litters born to these animals had been sired by the white males. In actuality. this was a study of the interactions between the two species *M. domesticus* (white) and *M. musculus,* and not necessarily the comparison between domesticated and wild house mice. Their results and discussion are completely consistent with the findings of Thuesen (1977) (Sec. V,B,2) on the social dominance of *M. domesticus* over *M. musculus*. Their work illustrates the point that misleading results may be obtained by not considering the taxonomic identity of the experimental animals.

B. Maintenance Behavior

The daily maintenance activities of the animal include a variety of behaviors related to moving about in the environment, fighting, mating, and building a burrow system. Available studies vary in their thoroughness and focus, ranging from anecdotal observation to an experimental, genetical orientation. More interspecific comparisons among the house mice would provide valuable data on the nature of behavioral changes during evolution.

1. Daily Activity Behavior

While the activity levels of wild *M. domesticus* are higher than in their domesticated relatives, Kavanau (1966) showed that the deer mouse (*Peromyscus maniculatus*) was much more active and versatile than the house mouse, as measured by wheel-running in cages. In a series of studies comparing the performances of many genera of muroid rodents, Dewsbury and his colleagues have studied a feral stock of *M. domesticus* for their open-field activity (Webster *et al.*, 1979), visual-cliff performance (Sloane *et al.*, 1978), climbing (Dewsbury *et al.*, 1980), and swimming behavior (Evans *et al.*, 1978). House mice showed relatively good depth perception, and scored high in climbing and swimming abilities.

2. Agonistic and Mating Behavior

The agonistic and mating behavior of domesticated, inbred mice has been comparatively well-studied (see reviews by Lagerspetz, 1964; Scott, 1966; McGill, 1970), but relatively little has been done with wild animals. The available data suggest that there is much intrapopulational variability in these important behavior patterns which are closely related to individual fitness and that there is a genetic basis for much of this variation. Thuesen (1977) studied the agonistic behavior of stocks of wild-caught *M. musculus* and *M. domesticus* from near their contact zone in Denmark. No qualitative differences in behavioral postures were seen, but there were quantitative differences: *M. domesticus* had more of the higher-level aggression components in its repertoire. Presumably because of these differences the *M. domesticus* were able to socially dominate the *M. musculus* when interspecific encounters were staged. He hypothesized that this more aggressive behavior favors *M. domesticus* in the contact area with *M. musculus*. Dominance behavior between *M. domesticus* and various species of *Peromyscus* mice was studied by Baenninger (1973). In the context of the interactions of these various species and the house mouse in nature, the results were ambiguous, e.g. whereas house mice always dominated *P. polionotus* in the staged encounters, it appears that the *Peromyscus* can drive out house mice in the natural habitats (see Sec. II,D,1). In contrast, there was no agonistic behavior recorded between caged specimens of the California harvest mouse (*Reithrodontomys megalotis*) and *M. domesticus* (Catlett and Shellhammer, 1962), and these two species live together in many habitats in California. Ebert and Hyde (1976) observed variability in agonistic behavior of females from a wild stock of *M. domesticus*. By selecting for high and low levels of this behavior, they were able to produce lines that were statistically significant from one another on the test after only four generations. These limited data suggest that genetic variation is present and that differences in levels of agonistic behavior could be expected between local populations if the environmental or social conditions favored one particular behavioral strategy over another.

Comparisons of the mating behavior in wild and inbred mice have been done by Estep *et al.* (1975), Dewsbury (1979), and

Complex tunnels connect the food cache and the nest chamber. Coupled with this physical structure is an elaborate behavioral system. The mice make the mounds in the fall, and they may even work in the daylight to quickly gather an adequate mound of seeds (Festetics, 1961). More than one mouse participates in making the food cache, but the exact genetic relationships among these workers is not known. During the winter, many mice are found in a single nest. As many as 19 were reported, with a modal range of 5–6 animals per mound (Mikes, 1971). The elaborate nature of this mound-building behavior, with its easily understandable selective advantages, makes this a system that should be much more closely studied with respect to the genetic relationships of mound groups.

C. Dispersion Behavior

Knowledge about dispersion behavior is important for any discussion of gene flow in mouse populations. What is known about the movement patterns and spatial organization of mice is derived from many types of studies: direct examination of the capabilities of mice to return to home areas after displacement; information gathered from mark-recapture programs on gridded study areas; observations on enclosed populations; and inferences based on the distribution of allozyme genotypes from carefully organized trapping programs. At present we only know about feral and commensal populations of *M. musculus* and *M. domesticus*. Comparative data for aboriginal species, such as *M. spretus*, would permit us to contrast the structuring of the derived, feral populations of commensal species with the presumed ancestral type. If good information were available on the rates of successful dispersal it would become easier to predict the emigration strategy of individuals living in different kinds of habitats or in populations varying in density. What is known about the dispersion behavior of mice is that they can recognize important parts of their home area, they can return to these sites after displacement, and conversely, they may migrate long distances. Home ranges vary broadly in size depending on the type of habitat, and social organization is variable.

1. Homing Behavior and Emigration

Within their home areas mice recognize important landscape features: Caldwell (1964) observed how resident mice immediately identified their environmental position after release from traps and ran directly to holes, whereas the mice scored as transients behaved erratically upon release and would hide in the first clump of grass that they encountered. Furthermore, mice are capable of returning to their home area after long-distance displacement. This implies that they have knowledge of a larger area than the home site, or they are able to find the area through powerful sensory capabilities. By capturing animals and displacing them for distances up to 250 m away from the trap site, Sims and Wolfe (1976) were able to study the homing capabilities of mice. They found that both sexes homed equally well, but that mice from the fields did better than mice captured in buildings.

Aside from their daily, short-term movements within home ranges, mice may make one-time, long-distance moves. A better understanding of this emigration behavior is essential for any discussion of the role of gene flow and genetic structuring of mouse populations. The available data is conflicting, in that long distance movements are known, but many studies repeatedly stress the small sizes of home ranges and the low frequencies of interchanges of animals between populations separated by short distances. Really long distance movements of individual *M. domesticus* have been reported: 1070 m (Pearson, 1963), 690 m (Caldwell, 1964), and 810, 920, and 2400 m (Tomich, 1970). These are record dispersal distances in populations where the average distances moved are much smaller, but they are suggestive of the potential for long-distance exchange between populations. The more typical observation is that there is comparatively little interchange (approx. 5%) of animals between study areas separated by small distances—on the order of tens of meters. In studies of an indoor population of *M. musculus*, 5 and 8% of the mice moved from the attic to out-of-doors or from the attic into downstairs rooms (Petrusewicz and Andrzejewski, 1962; Adamczyk and Walkowa, 1971). Only 12 of 500 *M. domesticus* living in a basement were subsequently trapped outside (Young *et al.*, 1950). Reimer and Petras (1968) found only 6% of the *M. domesticus* that they studied moved between corncribs separated by only a few meters. During 2 years of study, Massey and Vandenbergh (1980) report low levels (1.5%) of emigration in outdoor mice in North Carolina. Brown (1953) found no exchanges of animals between adjacent barns in Maryland. Although Tomich (1970) reported some long-distance dispersal of mice in Hawaii, he states that this was uncommon, and there was little movement of mice between adjacent grids in the same field. The highest reported rate of successful dispersal is that of feral *M. domesticus* on Skokholm Island, where Berry and Jakobson 1974) found that 20% of the breeding mice came from a site away from their natal area. From this very limited data on marked specimens, it appears that commensal mice do not move away from their birthplace as frequently as do feral animals. Thus the relative success of dispersers is not too well-known, and this makes it difficult to evaluate what risks the individual has in leaving a natal area and trying to become established in a new habitat. Under laboratory conditions, socially subordinate animals were the ones that emigrated most often (Butler, 1980), and these are exactly the animals whose chances for successful breeding are lowest in the home area (see Sec. V,C,3).

Many studies show that dispersal rates vary seasonally. In one experiment, the dispersal rate increased from 10–39% when a supplementary food source was removed from a basement population (Strecker, 1954). The dispersing animals were healthy, of both sexes, and included visibly pregnant females. Other studies show seasonal peaks. Dr. J. Pelikan (personal communication) observed marked, field-dwelling *M. musculus* immigrating into houses in Czechoslovakia in the autumn, and this behavior is reported for many populations of this species (Ursin, 1952; Serafinski, 1965). Whether the same individuals survive and return to the field habitat in the following spring is not reported. DeLong (1967) found a great increase in dispersal after the rains began in the autumn in *M. domesticus,* whereas Myers (1974) reported animals moving during the early spring in a nearby area. It is not impossible that on these two areas the periods of lowest food availability occurred at slightly different times and that food shortages can explain both cases of increased movement. Deteriorating habitat was certainly the basis for the long-distance dispersal of nearly the entire population of *M. domesticus* from one field to another in Maryland (Stickel, 1979). These dispersers also included animals of both sexes and all ages, but Myers (1974) found more females than males among the emigrants. She found that pregnant females were among those moving and that mice moved from the high-density to the low-density grid. In Australia, more long-distance dispersal was found among males than females (Newsome, 1969b). DeLong (1978) comments on how important dispersal is in determining the social structure of mouse populations. Since this opportunity to disperse is the essential difference between natural populations and most cage experiments, conclusions about social structuring in the latter situation must take this factor into account.

2. Home Range Behavior

The area in which the mouse spends most of its days is considered its home range. Daily movements of free-ranging *M. musculus* were studied in Kazakh, S.S.R., using radioactively tagged individuals (Nikitina *et al.,* 1976). The mice were active foragers and covered their entire home ranges from 2–13 times per day, travelling distances of 0.5–2 km daily. Estimates of home-range size in these short-term studies was 1100–2200 m^2. Most animals stay in one place throughout their lives, but occasionally an individual will shift its home range. Lidicker (1966) reports definite shifts in the home ranges of mice on Brooks Island. In the area studied by Newsome (1969b) in Australia, it appears that some mice actually migrate from reed-bed homes to a wheat field and back again as living conditions fluctuated in the agricultural habitat. But there is a definite, sedentary portion of a population that moves about a limited area. The size of the home range varies (Table IV). Generally home ranges are smaller among commensal mice than feral mice. But more than simply contrasting "indoor" versus "outdoor" habitats, this difference reflects in

Table IV

Home Range Size and Movement in *M. domesticus*

Locality	Habitat	Density	Sex (N)	Home range		Distance between recaptures (m)	Reference
				Area (ha)	Diameter (m)		
Maryland	Barn		M			6.1	Brown, 1953
			F			3.8	Brown, 1953
Wisconsin	Cellar	0.54/m^2	M			4.0	Young *et al.*, 1950
		0.54/m^2	F			3.4	Young *et al.*, 1950
Ontario	Barn					7.6–13.7	Reimer and Petras, 1968
	Corn crib					1–3	Reimer and Petras, 1968
	Agricultural fields					61–122	Reimer and Petrus, 1968
South Carolina	Fields		M(6)	0.19 ± 0.182			Caldwell, 1964
			F(7)	0.14 ± 0.053			Caldwell, 1964
Arizona	Agricultural fields	Approximately 5/ha			61(26.8–104)		Justice, 1962
California	Fields		Pop.I,M(2)	0.013			Quadagno, 1968
			Pop.I,F(6)	0.012			Quadagno, 1968
			Pop.II,M(5)	0.037			Quadagno, 1968
			Pop.II,F(2)	0.036			Quadagno, 1968
California	Brooks Island	580/ha and declining	Winter M	0.014 ± .0016	13.4		Lidicker, 1966
			Winter F	0.016 ± .0019	14.0		Lidicker, 1966
			Summer M	0.014 ± .0034	13.4		Lidicker, 1966
			Summer F	0.008 ± .0018	9.8		Lidicker, 1966
Guam	Fields	7.4–25/ha			50		Baker, 1946
Australia	Reed bed	Few–617/ha				7.9	Newsome, 1969b

large part the density of the food resources. For instance, in studies of Canadian *M. domesticus,* Reimer and Petras (1968) observed that the animals living in the cribs full of corn moved the least, whereas in the barns, where food was distributed more sparsely in the hay, movements were of intermediate lengths; in the agricultural fields the mice moved long distances. Mice living in the mixture of feces and discarded grain of chicken barns were estimated by Selander (1970a) to have home ranges of only a few square meters. But it does appear that some field populations have ranges of about the same size (7–10 m) as those of cellar and barn mice (3–13 m) (Table IV). One common aspect to nearly all of the studies is that males are reported to have larger home ranges than females (Table IV).

3. Social Organization and Population Structure

As a consequence of mouse–environment and mouse–mouse interactions, the animals will become distributed over the habitat in a certain manner, and the whole population will begin to have a characteristic "structure." The smallest functioning unit of a population will be the individual mouse who might have a completely random association with other individuals; in such a case there would be no structure through time. Of course, mice are not dispersed through their environment in such a random way, but the degree to which they are ordered is contested and of considerable importance for theories of population genetics. Many works on mouse populations were stimulated by the premises and conclusions about the behavior of *t* alleles (Sec. III,E). Mathematical studies suggested that if these deleterious alleles were to be maintained by chance factors at the observed frequencies, then local populations would have to be very tiny—on the order of 4–10 animals. Only under these conditions could the stochastic effects of sampling error be sufficiently great to override the purging tendency of natural selection against the carriers of *t* alleles. The mark and recapture studies and enzyme analyses of Petras (1967a,b) and Selander (summarized in 1970a) were directed at finding out the size of the breeding units (demes) in a "typical" mouse population. Their finding of small deme sizes offered support for the predictions of mathematical theory, which has worked its way into the form of a dogmatic characterization of mouse populations. DeFries and McClearn (1972) reviewed this type of social structuring of mouse populations. The data on the patchy distribution of polyoma virus (Sec. II,D,3) and *H-2* haplotypes (Sec. III,F) also suggest highly structured demes in commensal house mice. But there is considerable evidence that many mouse populations are not so tightly organized. Because there appears to be a wide range of variation in organization, predictions based on a single type of social arrangement are likely to be misleading. Appreciation of this variation is particularly important when making predictions about the behavior of processes that are highly dependent on chance factors, such as the distribution of deleterious genes or of certain types of infectious agents. Another aspect of population structuring has been ignored because of the prevailing view of a single type of social organization: that alternative selection regimes might affect individuals living under different kinds of distributional patterns.

Much work on the social structure of house mice was done with caged populations (Brown, 1953; Crowcroft, 1955; Crowcroft and Rowe, 1963; Reimer and Petras, 1967; Lidicker, 1976; Butler, 1980). The same types of social structuring have consistently appeared under these experimental conditions using both laboratory and wild stocks of mice, and we can consider the results to be of general significance. They support the idea of closed demes of mice. DeLong (1978) considered dispersal as critically important in determining spatial ordering of mouse populations, and the lack of this option, in experiments, makes it difficult to tell if or when this natural mechanism for limiting density and altering social encounters may operate to change social structure.

The cage studies, ranging from simple one-room environments to complex multichambered habitats mostly show that dominant males subdivide the area into defended territories. But Butler (1980) observed dominance hierarchies formed in small populations. Males will hold and defend territories even if no females are present (Reimer and Petras, 1967). In such an area, any other males, usually offspring, are subordinate. The tyrant male patrols the boundaries of his area and attacks and evicts most nonrelated intruders. Territorial males were found to be significantly heavier in weight than subordinate animals (Vessey, 1967). A number of females may live within the range of a male. In most, but not all, cases the females live inside of the territory of a single male (Butler, 1980). Both Brown (1953) and Vessey (1967) have observed females that ranged throughout the cage and even attacked and killed dominant males. However, most cage studies report that females remain with a particular male, and Lidicker (1976) observed them engaging in defense of the territory with the male. Lidicker (1976) described how such a rigid social system results in a fixed partitioning of the enclosed space, even as the density increased from 8 to 1000–2000 animals. As reproduction swelled the ranks of mice, offspring were constrained from moving out of their natal area and so each of the original territories came to contain more than 100 closely related mice. He was able to show that additional territories could be established only by placing new males in areas at the boundaries of two old territories. There was more success in introducing a new female than a male into the enclosures.

In a study of laboratory mice, DeFries and McClearn (1972) noted that socially dominant males sired most of the young. Wolff (1978), watching caged, wild-caught *M. domesticus*, observed that dominant males made only one-half of the matings when subordinates were present in the territory. But these

dominant males had 71% of the matings with the females that subsequently littered in their territory. He also noted that females actively solicit copulations only with dominant males. Lidicker (1976) noted that a distinctively marked, dominant male sired more than five litters with two females during a 100-day period. Oakeshott (1974) found that there was a slight positive association between male social position and mating success and that time of arrival in the colony was important in determining social rank. Thus dominant males have an apparent fitness advantage over subordinate males, and this justifies their aggressive defense of an exclusive territory under these environmental conditions of high food density.

As reported by Lloyd and Christian (1969) and others, the founding females in a deme do most of the breeding, and the rank of the female was related to her reproductive success. Urine of wild female *M. domesticus* was shown to have the same repressive affects on the onset of puberty of virgin female mice as seen under controlled conditions in the laboratory (Massey and Vandenbergh, 1980). What advantages accrue to a female who limits her movements to the range of a particular male were not too clear until recently, because none of the earlier studies reported that males pay any interest to the nestlings. The adaptive significance for such an association may now be explainable on the basis of the infanticidal behavior of male mice (Labov, 1980). This important study reports males killing offspring of females with whom they have not copulated or "fooled" into believing this to be true. Within a deme, composed of a dominant male, some breeding females and their offspring, there is much less aggression than observed between individuals belonging to other demes (Brown, 1953; Rowe and Redfern, 1969; Lidicker, 1976). It has also been shown by both Lloyd (1975) and DeLong (1978) that reproduction decreases in dominant females whenever the male territorial system breaks down and male–male aggression intensifies. This lowered aggression level is an additional advantage to the reproducing female living with only one male.

The toleration of the young in the territory by the parents, who nevertheless repress their reproductive maturity, is taken for granted in *M. domesticus*. It should be pointed out, however, that this is not a universal behavior in rodents, and there are other parent–offspring strategies: in the rice rat (*Oryzomys palustris*) the juveniles are attacked and killed when they become reproductively active in population cages (Lidicker, 1965). In a species such as this, a large family group would not be expected to exist under field conditions because of this intolerance.

Under natural conditions, it is much more difficult to get such detailed knowledge of the social, spatial, and genetic relationships of an entire population: there is a high mortality rate; nestlings cannot be marked until after they are weaned; direct observations of interactions are usually impossible; and larger home ranges make trapping programs logistically difficult. As a consequence, our understanding of the degree and duration of social units in wild populations is more tentative. Most field studies report much less evidence of tightly organized populations; but given the great rates of change taking place in important environmental characters such as temperature, nest site, and food resource availability, it is not surprising that feral groupings appear more ephemeral. From the study of Baker (1981), it appears that even chicken-barn populations may be more labile in structure than indicated by Selander (1970a).

There is evidence from three studies that suggest that populations sometimes consist of two segments that differ in their movement and, presumably, social patterns. A population of *M. musculus* studied in an attic was composed of residents and transients (Petrusewicz and Andrzejewski, 1962; Wierzbowska and Petrusewicz, 1963). The transients, forming 30% of the trapped mice, were found in the attic during only one trapping period. In the old-field populations of *M. domesticus* in South Carolina, there were also resident and transient groups (Caldwell, 1964), and the Australian wheat-field population studied by Newsome (1969a) seems best characterized as transients.

Resident field populations sometimes do have social structure. Myers (1974) found adult males to be overdispersed on the trapping grids, whereas adult males and females were distributed in a random way with respect to one another. This suggests that males space themselves in a manner consistent with mutually exclusive territories. Myers found that during periods of high population density animals could not be introduced into the area but that this was possible at lower densities. This implies that social forces were operating to exclude invaders at high-population levels. In the Skokholm Island population, Berry and Jakobson (1974) found that resident males on the cliff area had discreet, nonoverlapping home ranges. At the beginning of spring breeding, the female home ranges overlapped those of different males, but later in the season they came to be included within those of a single resident male. At the very low densities of 5 mice per hectare, Justice (1962) found no evidence of any family structure in field populations in Arizona. Stickel (1979) observed that after a general move of about 200 m by a mouse population more than 30% of the original living groups were maintained in the new field. This seems to be a much higher than expected degree of association by random chance and implies considerable social cohesiveness in these outdoor mice. More information is needed on the degree of co-association between individuals in these wild populations to understand how much structure is present in these environments. Most of the previous studies do not analyze the recapture data in proper terms for understanding social organization. The data reporting low levels of movements between nearby populations (Sec. V,C,1) suggests that local demes replace themselves largely from among their

own progeny. But Berry and Jakobson (1974) note that a minimum of 20% of the breeding females on Skokholm Island breed at a site different from where they were born. For any significant amount of inbreeding to occur in demes of feral populations, immigration rates would have to be much lower than this.

VI. REPRODUCTION: INTENSITY AND REGULATION

Reproduction is the key to the survival of any species. As an activity of the individual, it determines the ultimate fitness of that particular genotype and is effected by internal regulation (hormones, nutrition, stress, etc.). As a populational phenomenon, it becomes a major factor in determining the survival of the group. At this level, which concerns population dynamics, questions about the differential success of the individual are generally subsumed into average measurements. Nearly all studies of mouse populations to date have dealt with reproduction from the viewpoint of its role in population growth and regulation. Some recent reviews and major research articles that discuss reproduction primarily in the context of population dynamics include Berry (1970), Pelikan (1974), Newsome *et al.* (1976), Lidicker (1976), Stueck and Barrett (1978), and DeLong (1978). As a result of these and many other such studies, we have a very good understanding of the average behavior in mouse populations. We understand some important determinants of population growth and decline. But there has been little discussion of what options are available to individual mice for increasing their reproductive success, despite the great amount of documented variation in many important reproductive factors. In my review of the closely interrelated subjects of Reproduction, Demography, and Population Dynamics, I shall try to emphasize the variation seen in characters that can have important consequences for the fitness of the individual mouse. From this viewpoint, interesting questions about the evolution of adaptive strategies, such as a commensal versus wild existence, can be developed.

An excellent review of the reproductive ecology of the house mouse has been published by Bronson (1979a). He outlines the proximate factors of behavior and endocrinology that affect the reproductive activity of the individual and control the interactions of larger groups of animals. His work describes, in detail, many of the points made here. I will stress the variation in reproductive parameters reported in mice and the bases of that variation. Table V summarizes the published reports on the intensity of reproduction in house mouse species. I have included some data from my laboratory stocks, derived from wild-caught specimens, for additional information on variation.

Table V

Litter Size and Embryonic Resorption in House Mouse Species

Species	Locality	Habitat	Season	Adult female size (gm)	Litter		Embryos resorbed (%)	Reference
					Number	Size		
M. abbotti	Georgia, S.S.R.	Outdoors	Spring–autumn			8		Kochija, 1960
	Yugoslavia, Gradsko	Lab			16	5.1(1–8)		R. Sage, observation
M. hortulanus	Ukraine, S.S.R.	Outdoors	Spring–autumn	>12	55	7.4(4–11)		Naumov, 1940
	Yugoslavia, Vojvodina	Outdoors		9–15	56	7.3(2–15)		Mikeš, 1971
	Yugoslavia, Pančevo	Lab			18	6.7(4–9)		personal observation
	Austria, Halbturn	Lab			9	6.3(2–9)		R. Sage, observation
M. spretus	Morocco, Azrou	Lab			28	5.6(3–9)		R. Sage, observation
	Spain, Pto. Real	Lab			17	5.8(3–9)		R. Sage, observation
M. molossinus	Japan, Kyushu	Indoors and outdoors	March–August		37	5.1	10.4	Hamajima, 1961a,b
			September–February		44	6.4	2.7	Hiraiwa and Hamajima, 1960b
M. castaneus	Malay, Kuala Lumpur	Indoors		9–12	82	4.3(1–7)		Harrison, 1955
	Burma, Rangoon	Indoors		13.3	64	4.5 ± 1.3		Walton *et al.*, 1980
	Thailand, Thon Buri	Lab			11	5.6(3–8)		R. Sage, observation

(*continued*)

Table V—*Continued*

Species	Locality	Habitat	Season	Adult female size (gm)	Litter		Embryos resorbed (%)	Reference
					Number	Size		
M. musculus	A.S.S.R., Yakutsk	Indoor(#1)	May	>22	17	8.6		Romanova, 1970
		Indoor(#1)	September	>22	56	9.0		Romanova, 1970
		Indoor(#2)	September	>22		8.4		Romanova, 1970
	U.S.S.R., Moscow	Indoor	All year		486	5.9		Tupikova, 1947
		Outdoor	Spring–autumn		10	9.3		Tupikova, 1947
	Yugoslavia, Belgrade	Lab			39	5.5(1–10)		R. Sage, observation
	Czechoslovakia, Moravia	Indoors	All year	17.4	183	5.6 ± .12(1–10)	1.1	Pelikan, 1974
		Outdoor: haystacks	All year	16.8	58	6.3 ± .19(3–9)	1.4	Pelikan, 1974
		Outdoor: fields	Spring–autumn	18.3	67	7.8 ± .19(4–12)	1.9	Pelikan, 1974
	Czechoslovakia, Bratislava	Lab			19	6.8(2–11)		R. Sage, observation
	Czechoslovakia, Brno	Lab			39	6.3(3–12)		R. Sage, observation
M. domesticus	Israel, Jerusalem	Lab			37	4.9(1–9)		R. Sage, observation
	Morocco, Erfoud	Lab			27	3.8(2–9)		R. Sage, observation
	Morocco, Azrou	Lab			34	5.6(1–11)		R. Sage, observation
	Yugoslavia, Metkovič	Lab			26	5.4(2–8)		R. Sage, observation
	England	Indoor: urban houses		15.2	95	5.2 ± .18(1–10)		Laurie, 1946
		Indoor: flour mills		16.1	158	5.5 ± .13(1–11)		Laurie, 1946
		Indoor: cold room		20.5	137	6.4 ± .20(1–12)		Laurie, 1946
		Outdoor: haystacks		14.4	186	5.8 ± .11(2–9)		Laurie, 1946
		Outdoor: haystacks						
		low density			84	6.2 ± .20	1.6	Southwick, 1958
		medium density			125	5.7 ± .15	2.2	Southwick, 1958
		high density			267	5.6 ± .10	1.7	Southwick, 1958
		very high density			73	5.1 ± .20	2.0	Southwick, 1958
	Isle of May				37	6.5	5.0	Batten and Berry, 1967
	Pembrokeshire	Barn			14	6.2	9.2	Batten and Berry, 1967
		Haystack			65	7.3	2.7	Batten and Berry, 1967
	Skokholm Island	Outdoor			58	7.5	4.1	Batten and Berry, 1967
		Lab			244	5.6		Batten and Berry, 1967
	U.S.A., S. Carolina	Outdoor: Fields			19	5.7		Caldwell, 1964
	U.S.A., Mississippi	Indoor: Food handling buildings	All year		174	5.0 ± .12		Smith, 1954
		Indoor: urban houses	All year		69	4.9 ± .17		Smith, 1954
		Indoor: other buildings	All year		43	4.3 ± .19		Smith, 1954
		Indoor: farm buildings	All year		6	3.7 ± .17		Smith, 1954
	California,							
	Orinda	Grassland	Spring–autumn		43	5.7		Pearson, 1963
	Tilden	Grassland			32	7.4		Pearson, 1963
	Bay Area	Field			19	6.1(4–9)		Quadagno, 1967
	Brooks Island				6	2.2		Lidicker, 1966
	Guam Island	Indoors and outdoors		9–12	—	3–5		Baker, 1946
	Marshall Island, Enewetak	Outdoors		9–10	6	4.0		Berry and Jackson, 1979

Some patterns are apparent in Table V. The aboriginal mice, *M. abbotti* and *M. hortulanus*, have large litter sizes ($\bar{X} \geq$ 7–8). In the laboratory colonies of these species, the averages drop to a slightly lower level ($\bar{X}$ = 5–6, see Table V). The commensal species with the highest average litter size is *M. musculus*. Russian populations have 8–9 young per litter. In Czechoslovakia, the litter size ranges from 5–8, depending on the habitat. In my laboratory populations, the averages are still high (see Table V), and litters of 10 or more young occur with some regularity. Within *M. domesticus*, there is a great variation in litter sizes across its present range. The averages and extremes are generally lower than in the three species just discussed. In England, litters range from 5–6 depending on the habitat. In the California grasslands, the average numbers of young are fairly high, except for the Brooks Island population. In warmer habitats, e.g., Mississippi, Guam, and Enewetak Island, litter size is low. My laboratory populations of this species also have smaller litters than the *M. musculus* stocks living in the same room. Extremely large litters occur much less often in this species. Of 576 litters examined by Laurie (1946), only 12 of these had 10 or more young, and 9 of these cases involved cold-store mice, which have the highest average litter size. In my laboratory stocks of *M. domesticus*, there has only been 1 in 124 litters that had more than 9 young. In tropical Malaysia, *M. castaneus* has few young per litter.

There is an obvious trend in litter size variation in this field data: populations of mice from cooler environments have larger litters than animals from warmer sites. This is true on a local level, e.g. English *M. domesticus* from cold-storage rooms versus other, warmer dwellings, and Czechoslovakian *M. musculus* from fields versus houses (Table V). On a larger scale, the high litter sizes in the coldest parts of Russia ($\bar{X}$ = 8–9), versus low litter numbers (3–4) in tropical habitats demonstrates the extreme limits to which this process can reach. The differences in litter size between the laboratory stocks of Moroccan *M. domesticus*, collected at the Saharan desert town of Erfoud ($\bar{X}$ = 3.8) and the cooler, mountain locality of Azrou ($\bar{X}$ = 5.6), may reflect this same relationship between litter size and relative warmth of the native habitat. Although there are average differences in litter sizes between local populations, there are also within-locality, seasonal changes (Pelikan, 1974; Rana and Beg, 1976). Average litter size ranged from 7.3–8.3 in field-caught, and from 4.9–6.1 in house-caught *M. musculus* in Czechoslovakia. In this species, the within habitats trend is for higher litter sizes in the warmer, summer season than in the cooler periods, and so the trend runs counter to the larger scale pattern. But in *M. domesticus* in Pakistan, litter size is lowest in the summer ($\bar{X}$ = 5.4) and rises to 7.0 in winter and 8.3 in the spring (Rana and Beg, 1976).

The ultimate basis for this observed variation in litter size is unknown, but in laboratory experiments, it is possible to replicate trends observed in the field. Barnett *et al.* (1975) summarized their results of raising feral *M. domesticus* stocks in low (−3°C) and high (21°C) temperature environments. After 10 generations there was a highly significant difference in average litter size of mice from the cold ($\bar{X}$ = 8.2 young) versus warm ($\bar{X}$ = 5.2 young) environments. This difference probably has a genetic basis, as mice transferred from the cold to a warm room continued to have large litters. Pennycuik (1979) tested stocks of mice living at hot (32°–34°C) versus warm (21°C) temperatures. Average litter size was much lower in mice from the hotter environment, but there was a gradual increase in reproductive performance of these mice after some generations of breeding. This parallels the field observations of low-litter sizes of mice from tropical environments. The range of average litter size in the wild mice encompasses that found in inbred lines (Altman and Katz, 1979). It is known that litter size varies with the number of litters born to a particular female (Snell, 1941; Franks and Payne, 1970) with highest litter sizes in the middle portion of the life cycle. Falconer (1960) showed high heritability for litter size in laboratory mice. So, while some of the variation seen in wild populations may reflect seasonal variation in food quality and/or differential age composition of the breeding population, it is likely that there is a genetic component to this variation. It may be that on a local scale mice of particular genotypes may be more favored in warmer (usually commensal) than cooler (feral) habitats.

VII. DEMOGRAPHY

Within the truism that "all mice must die," lies the critical point of "when" this happens. The time between birth and death varies among individuals, and this variation is important: both as it affects individual fitness as well as the growth rate of the population. Other things being equal, when births exceed deaths, the population increases in number. When the birth-death ratio varies between the sexes, then the population sex ratio may become distorted; when groups having different genotypes show variation in survival time, then evolutionary changes occur.

Mice of inbred strains have average life spans ranging from 500–800 days (Staats, 1980). Very few free-living wild mice reach-this age, but they can survive this long in captivity: 1.5% of a large sample of wild-caught *M. domesticus* were still alive after 30 months (900 days) of captivity (Gardner *et al.*, 1974). Indeed, a study of aging in wild mice (Barnett *et al.*, 1974) concluded that there were few pathological changes associated with advanced age. There were some signs of interstitial nephritis in about one-half of the individuals, but these authors state that "the biologically important changes associated with ageing of female mice are in the reproductive system" (p. 279). Maximum life spans for free-living individuals in marked populations are less than 18 months: 12 months (Caldwell, 1964); 15–16 months (Berry, 1968), 15 months

(Reimer and Petras, 1968), 14 months (Tomich, 1970), 17 months (Stickel, 1979). The mean survival time of most animals is much less than this, although good statistics are uncommon. The measures are further confounded by the underlying sexual and seasonal pattern of variation in survivorship. Embryonic mortality is on the order of 5–10% (Batten and Berry, 1967; Table V). Death during the nestling stage can be high under crowded conditions. Decreased nestling survivorship is part of the syndrome of declining population growth noted in all enclosure studies. Under much lower densities in the field, this type of death may be much less, but measurements are absent. Field estimates of survivorship can begin only after young animals leave the nest and enter the trappable population. Even then there are very few data on survivorship: an attic population of *M. musculus* had a mean residency time of 73 days (Petrusewicz and Andrzejewski, 1962); in a barn population of *M. domesticus* this mean duration lasted from 40–76 days, respectively, for males and females (Brown, 1953); and in outdoor enclosures this value was 20–38 (males) and 32–40 (females) days (Stueck and Barrett, 1978). Data is insufficient to make anything more than a provisional conclusion that indoor mice seem to live longer than field mice.

All but one of the population studies show that females survive longer than males (Petrusewicz and Andrejewski, 1962; Brown, 1953; DeLong, 1967; Newsome, 1969b; Berry and Jakobson, 1971; Stickel, 1979). Only Baker (1946) concluded that males may do better than females. DeLong (1967) and Newsome (1969b) estimate monthly survival rates of feral mice of different sex and age. They observed adult mice surviving better than juveniles during the increase phase of the population growth cycle, and earlier resident adults did better than late arrivals when the mortality rate greatly increased at peak population density. Alteration of demographic patterns by the application of a rodenticide was attempted by Emlen *et al.* (1958), but no obvious differences were detected between the control and experimental populations. There is really so little information on demographic parameters to make any definitive statements: no mark–recapture studies of aboriginal species have been done; comparisons of local populations of *M. domesticus* living under feral and commensal life styles are lacking; and experimental manipulations are almost nonexistent.

One interesting pattern of variation in sex ratio is seen in mouse populations. In large collections, the ratio is about equal, with a very slight preponderance of females. But a decided bias appears if samples are taken from populations of different densities. Generally, low density populations have more males than females, but the reverse is true at higher levels. Thus, Pelikan (1974) reports 47% males from buildings, 49% in ricks, and 53% in field populations of *M. musculus*. In a similar study of *M. domesticus* in Canada, Reimers and Petras (1968) found the sex ratio nearly equal in barns, but 3 times as many males as females were present in the low-density field sample. As a population of *M. domesticus* in a haystack grew in size, Newsome (1971) documented an increasing percentage of females over males: 10-month old population (52% females) versus 11–16 month old (87% females). Such changes arise because of the higher survivorship of females after they become members of the adult population.

There may also be a bias in the sex ratio of weanlings, and this suggests that females may be controlling this aspect of their reproduction. In the first litters produced in the springtime on Skokholm Island, the sex ratio is 70% in favor of the males, but declines to 47% by the end of the season (Berry and Jakobson, 1971). Rowe *et al.* (1964) found higher numbers of juvenile males than females in low density corn ricks. In enclosed populations, both Crowcroft and Rowe (1957) and Lidicker (1976) reported more males in the earliest litters produced by the founding pairs. The first two litters produced by the founders of a large enclosure population consisted of 11 males and 4 females (Lidicker, 1976). In these two studies the density was low when the males were most predominant. DeLong (1978) reported the ambiguous finding that the sex ratio of nestlings in his various experimental cages matched the frequency of the dominant sex in that particular cage. These repeated findings of distorted sex ratios under both experimental and natural conditions suggests that females are manipulating this feature of their reproductive behavior. It would be evolutionarily sensible for the female to invest her energies in producing offspring that will have the greatest average fitness in the next generation. I speculate that with the rapidly changing quality of the habitat as populations increase in density, the relative fitness of the two sexes may shift and females could try to increase their reproductive success by tracking this change.

VIII. POPULATION DYNAMICS

The reproduction, survival, dispersion, and dispersal of a group of associated mice combines to produce the dynamics of a local population. This population has a series of attributes different from individual behaviors, i.e., a growth and decline rate and extinction. The cycle of a growth phase, a peak, and a decline, are largely determined by the relative balance between the birth–death ratios of the individual mice. As the numbers of births (plus immigrants) exceeds the numbers of deaths (plus emigrants), the population grows, and a decline sets in with the reversal of this ratio. The complex array of interacting factors affecting reproduction, mortality, and dispersal have already been discussed in the preceding sections. Here I will review how these processes come to produce changes in the dynamics of the local population.

A. Habitat Change

Certain environments are more favorable to house mice than others: ranging from uninhabitable, to marginal, to optimal sites as conditions dictate. Because of an apparent need for an open grassland environment, populations of the mound-building *M. hortulanus,* are now greatly affected by agricultural activities. The development of huge, mechanized cooperative farms in eastern Europe has produced large environments of seasonally favorable living space, but with autumn plowing the mounds are destroyed and the winter food cache is lost. In the Puztas of central Hungary, where mound-building mice were abundant in the last century, they are now uncommon (Vasarhelyi, 1958). The successional cycle of abandoned agricultural fields in the southeastern United States makes these areas suitable for *M. domesticus* populations for only a certain segment of this environmental sequence (Caldwell, 1964; Briese and Smith, 1973). In the naturally occurring, fire-maintained vegetation of southeastern Australia, conditions are favorable for high population densities of mice only during the early years following a burn (Newsome *et al.,* 1975). The rick-building behavior of European farmers annually provides an ideal temporary habitat for populations of *M. musculus* and *M. domesticus.* Construction of buildings within a forest will make an otherwise unsuitable environment adequate for a commensal mouse population. In such diverse ways, the quality of habitats for mice can change over short or long periods of time. One of the traits characteristic of *M. domesticus* is its success at finding these newly available habitats and establishing populations in a very short period of time. For this reason it is an excellent example of a "fugitive species."

B. Seasonal Dynamics

After colonizing a habitat that is at least marginal or is favorable for increased births over deaths, a population cycle begins. The annual cycle of primary productivity is the ubiquitous environmental regulator of population growth for outdoor populations. As food resources become available in the spring, reproduction starts in the mice. Warming temperatures cause a decline in cold-induced mortality (see Sec. IV,A). Low densities of mice mean that there is comparatively little social repression of reproduction, and a decreased chance that contagious diseases can pass between individuals. With adequate cover and good nest sites, it is probably very unlikely that vertebrate predators can impose a mortality rate sufficient to keep the mouse population from growing. Pearson (1963) noted how cats preferentially preyed on the vole (*M. californicus*) until these were reduced to very low numbers before switching to mice as a major food item. At this time in the population cycle, the rate of reproduction is probably at a maximal level or is being directly regulated by availability of food. Access to a new store of food can initiate this same maximal rate of reproduction for a commensal population at any time of year.

With increasing numbers of mice, the socially-mediated repression factors begins to predominate. A decreasing proportion of the female population reproduces, but it is important to remember that these are largerly the same animals who were active in the early stages of the cycle. The founders show better than normal survival throughout this growth phase (DeLong, 1967; Newsome, 1969b), perhaps because they have obtained the "best" home range positions with respect to food abundance and nest security. Whereas variation in the quality of the home range is frequently studied in birds, it has not been specifically studied in mice. On Skokholm Island, it is clear that the central low-lying area is inferior to the rocky higher ground around the periphery for year-round home ranges, as during the winter most of the mice in the center of the island die (Berry, 1968).

Ultimately, the reproduction of most females is socially repressed because of high density effects. It may also be at this time that food resources become a limiting factor on the remaining reproductively active females, simply because of the increased demands by the surviving nonreproductives. Newsome (1969a) describes a case where he felt that a wheat-field population, at peak density, was limited by the food supply. But the relative contribution of food as a limiting factor on reproduction is probably less than social repression at peak population densities. This has to be the case in the commensal and experimental populations. Such high densities, where almost no female is reproductively active, represents the extreme condition in wild populations. These high-density populations are stable, in that they continue at this level until food runs out or a density-dependent, contagious disease enters the population.

But most feral populations, such as described by Pearson (1963), DeLong (1967), and Newsome (1969b), begin declining without deaths from disease and without achieving superhigh (plague) densities. These typical annual declines of populations probably reflects increasing deaths resulting from the combination of both food limitation and climate-induced mortality due to the changing seasons. Again, during the decline phase of the cycle, established adults survive better than younger progeny although the absolute numbers of these oldest mice is now down from their high numbers during the growth phase. The inclement winter season takes a severe toll on feral *M. domesticus,* and this is probably the case for the other species as well.

Population decline to extinction is infrequently reported but, I think, is of great interest. The extinction of the Brooks Island mice was discussed in an earlier section (Sec. II,D,1). The

very finality of this event emphasized the role of interspecific interactions in determining the occurrence and density of house mice. This is a model case for biotic control of the niche width of an animal species.

Two other cases of population extinction are worth mentioning. Evans (1949) and Petrusewicz and Andrjezewski (1962) report on populations (*M. domesticus* and *M. musculus*) declining to extinction. These were followed by long periods of habitat desertion and the subsequent reestablishment of new populations. These populations were living indoors where there was no significant predation, and adequate food resources were present throughout the decline and vacancy phases. Cessation of reproduction was complete among the females, even though densities in the last trapping periods were very low. At this time, one would not expect social repression to still be controlling reproduction.

Exactly why these populations went extinct was not discussed, but I think some speculations are worthwhile. An explanation that might explain these cases and be consistent with what we know about wild mouse biology is the following: founding females produce most of the colony offspring, repress their daughters, and survive well in the most favorable home ranges. With advancing age, only their reproductive capabilities are impaired, not their social standing. Under this model, such old females might survive long enough to repress their own offspring long enough that they too lose their physiological capability to repopulate the area. Thus the chain of recruitment of young into an aging population would be broken and extinction would follow. This model stresses the important role that individual female social behavior may have on the survival of a population. Whether or not this is the right interpretation, these cases of "voluntary" extinction of demes need an explanation, as they represent significant evolutionary mistakes for the animals who choose to remain in these habitats rather than disperse. For a general review of social manipulation for evolutionary advantage, see Wilson (1975).

C. Annual Fluctuations and Plague Populations

The seasonal cycle of population growth just described has year-to-year fluctuations. This variability, overlaying the shorter annual cycle, results in higher or lower limits to the normal pattern. Berry (1968) notes a strong correlation between the coldness of the winter temperatures and the largest size reached by the population in the following breeding season on Skokholm Island. The critical cold period seems to come during February. He found that mild winter temperatures historically resulted in mouse "highs" at the lighthouse on the island. An outbreak of native mouse species and *M. domesticus* in Chile was attributed to unusually heavy rains during the preceding autumn and winter—a result of the "El Nino" ocean current (Pefaur *et al.*, 1979). Pearson (1963) correlated the outbreaks of *M. domesticus* in the San Francisco Bay region with unusually warm winter temperatures during the preceding 2 years, and he noted that such weather preceded the plagues of mice in Kern County and at Davis, California. Both authors speculate that reduced winter mortality left the spring populations at higher starting levels, which subsequently resulted in higher summer densities. In Australia, where mouse plagues also occur, Saunders and Giles (1977) found that they took place within 2 years after major droughts ended. They explained the highs coming at this time because of the release of the populations from predation pressure. They speculated that the drought affects the predator population more severely than the mice, and results in the latter building up numbers to a level where they "escape" control by predation. However, Newsome (1970) was able to experimentally induce plague populations with supplemental feeding when sufficient rainfall kept the soil moist.

Whatever processes produce these plagues, they are well-known widespread, and worthy of description. Fenyuk (1941) described them in southeastern Russia. It is not clear whether an aboriginal or commensal species is involved in these Russian plagues. Hall (1927) and Piper (1928) described the great plague of *M. domesticus* that occurred in Kern County, California, in 1926–1927. This epidemic lasted nearly 4 months, and affected an area 18 miles in diameter. Densities were estimated at 6 mice per square meter or 60,000/hectare (24,000/acre). Extrapolation to the total infested area puts the population size at nearly 4 billion mice. A more meaningful appreciation of this mouse density comes from their reports that 4000 pounds of mice were killed in one day in one grain barn, or that 3500 mice were visible at one time in a grain bin. Clearly these are populations where factors regulating reproduction were not operating at normal densities. What stimuli produced the overproduction is not known, and such an outbreak has not reoccurred in that area. But by the time the mice reached these numbers and began to run about in the daylight, they were doomed. Predatory birds migrated into the area and ate many, and large numbers died of disease (see Sec. II,D,3). Disease also acted on two other outbreak populations at Davis (Evans, 1949) and in Tilden Park, California (Pearson, 1963). Ryan and Jones (1972) provide a description of the dynamics of a more recent mouse plague in Australia.

IX. FIELD TECHNIQUES AND CAPTIVE PROPAGATION

The information presented in this review has come largely from studies of free-living animals. Although much has already been discovered about these wild ancestors of the domes-

ticated inbred mice, I hope that it is clear from my comments in the earlier sections that many questions are still unanswered. Techniques for carrying out good field studies of house mice are basically simple, but the care of the wild mice in captivity is slightly more difficult than required for domesticated strains.

A. Field Techniques

Suitable traps are the basic equipment needed for field studies of mice. Depending on the kind of study planned, some techniques of trapping are more appropriate than others. Recent general reviews dealing with techniques of small, wild mammal study are: Delany (1974), Twigg (1975a,b,c), Flowerdew (1976), and Golly *et al.* (1975). These works provide reviews of field methods: types of traps, methods of handling and marking wild mice, techniques for estimating natality, mortality, age structure, home range size, and population density. Delany (1974), Golly *et al.* (1975), and Snyder (1978) deal in part with the larger questions of general ecological theory as it relates to small mammals. In Chapter 2 of this volume, Marshall describes how standard museum study skins of mice are made. Fortunately house mice are comparatively ideal subjects for field studies: they are nearly ubiquitous in occurrence, generally unprotected by governmental restrictions, and easy to trap. Although there are reports on the occurrence of trap "shy" and "prone" animals in populations (Young *et al.*, 1952; Crowcroft and Jeffers, 1961; Reimov *et al.*, 1968), the numbers of these animals is not large, and they probably do not greatly bias the results of mark–recapture studies. Stueck and Barrett (1978) did not find social rank affecting trappability, and there was only a nonstatistically significant predominance of males over females in their traps.

Two types of traps and three models are suitable for the usual types of field studies. If information is needed on "instantaneous" events, such as density, morphology, reproductive condition, food habits, or internal parasites, then killing with snap-traps is appropriate. The readily purchased, common snap-trap is somewhat less desirable than the specially designed "museum special" trap (Woodstream Corporation, P. O. Box 327, Lititz, Pennsylvania, 17543), because the smaller size of the former trap frequently crushes the skull. There are two types of live-catch traps that are widely used, and each offers distinctive advantages. A box trap, with a spring-operated door is available in a rigid or collapsible model (H. B. Sherman, P. O. Box 683, DeLand, Florida 32720), and there is a larger two-chambered trap that allows for the inclusion of nesting materials in the inner box (Longworth Scientific Instruments Co., Ltd., Radley Road, Abingdon, Berkshire, England). The Sherman traps are useful because of their smaller size and lighter weight. In warmer areas these work satisfactorily, and there is little mortality caused by exposure to nightime temperatures. The Longworth trap has room for additional materials in its interior, where the mice can make a nest if temperatures are cold. These traps have been used in the long-term population studies reported by Lidicker (1966), DeLong (1967), Berry (1968), and Newsome (1969a,b). Dry, rolled-oats makes a very adequate bait for live traps, and this can also be moistened and stuck on the trigger bar of snap traps. Pieces of carrot or potato are attractive baits to mice living in particularly dry environments. Mice are most easily released from live traps into a clear plastic bag, where they can then be easily constrained and caught by hand. Away from the laboratory mice can be maintained in pint-sized canning jars, with pieces of hardware cloth cut to fit inside the ring lids. I have had very good luck in keeping wild mice in temporary cages manufactured from pieces of heavy-duty window screen. Pre-cut pieces of this screening (about 1 sq ft) can be carried flat in a suitcase and then rolled into tubes and closed up with staples. With a tube of newspaper, some cotton, pelleted mouse diet, and a piece of carrot or potato as a source of moisture, I have successfully transported mice all about Europe and North Africa, and returned them to the United States with only a very mimimum mortality.

B. Captive Propagation

Wild mice are relatively easy to keep in the laboratory if consideration is given to their differences from domesticated strains. Comments and suggestions on their peculiarities and appropriate handling techniques are found in Schneider (1946), Hiraiwa and Hamajima (1960a), Andervont and Dunn (1962), Evans *et al.* (1968), Wallace and Hudson (1969), and Bronson (1979b).

My experiences with many species of *Mus* supplement these published accounts. Survival of wild mice in the laboratory is good, but the major problem seems to be in getting them to breed regularly. Different species have different behaviors that provide minor difficulties. In my experience, the wild animals do not seem to be affected by disease. However, wild-caught animals should never be introduced into a laboratory colony without first being quarantined and carefully examined for murine pathogens. Each new addition of wild caught animals or animals from other colonies where the disease status is unknown must be examined. Handling wild mice requires a different strategy from that used for domestic strains. Wallace and Hudson (1969) describe special cages and a cage-cleaning apparatus that reduces the time required for maintenance. I have used the standard plastic cages, in small (28 × 17 × 12 cm) and medium (35 × 30 × 16 cm) sizes to house mice. To overcome the major behavioral feature that distinguishes them from domestic mice—jumping—cages are changed inside of a deep box. I generally do not handle my mice, but transfer them

using a tall, thin bottle. They are easily coaxed into a bottle and then moved to a new cage without alarming them. Because mice are naturally shy animals, I think that they are more secure with a nesting chamber in which they can hide. Tin cans of the right size serve very well for this purpose. They can be purchased from commercial companies in large numbers, are relatively inexpensive, can be washed and reused, and are not destroyed by the mice. All of the house mouse species use them for nest retreats, but some of the other species of *Mus* (*M. pahari* and *M. saxicola*) definitely prefer to construct their nests outside of the cans. Bronson (1979b) has recently shown that wild *M. domesticus* breed better in total darkness than in a lighted room, and I think that the cans provide that measure of preferred darkness in a normally lighted mouse room.

Schneider (1946) and Andervont and Dunn (1962) comment on how difficult it was for them to breed *M. domesticus* until they added running wheels to the cages. The exercise, as much as 10–15 miles of running per day by females (Schneider, 1946), caused them to come into estrous and begin a normal breeding cycle. The various wild house mice that I have collected (*M. abbotti, M. hortulanus, M. spretus, M. musculus, M. d. domesticus, M. d. praetextus,* and *M. poschiavinus*) have not shown this reluctance to breed without a running wheel. Only a few individuals *M. d. praetextus* have not bred. Otherwise most of them are extremely prolific breeders in my colony. As has been demonstrated in the laboratory studies, the *M. domesticus* show anoestrous behavior and nestling cannibalism under conditions of increasing population density in cages. I think that this behavior is the result of disturbances, from any source, intraspecific as well as environmental. I believe that breeding by wild mice in laboratories may be discouraged by high light levels, too frequent cage cleaning, and generally high levels of human activity in the colony room. Chipman and Fox (1966) found that handling, exciting, or distributing wild *M. domesticus* depressed pregnancy rates to the same degree as did the Bruce ("strange male") effect. Wild mice do very well when left alone.

Levels and types of aggression differ among species of *Mus*. The aboriginal species and *M. molossinus* seem to be the most retiring species of the complex, while *M. musculus* are definitely the most phrenetic. Aggression between young males is serious in some cages but not in others, and in the earliest stages consists of biting the tail. The onset of fighting probably is coincident with age of sexual maturity of the males. I keep my mice as single breeding pairs. The few attempts at polygamous matings have sometimes resulted in the death of the extra females or the male. I have found almost no instances of regular cannibalism of young mice except when too many animals are left in a cage. This is surely a pathological behavior that probably results from disturbing mice during an early stage of the life of the young animals. Andervont and Dunn (1962) found that most breeders could serve as foster mothers, since they are excellent parents.

All of the species of the house mouse complex seem to breed readily with their littermates, in spite of the tentative evidence of preferences for other mating partners (Mainardi, 1963; Yamazaki *et al.*, 1976). I have not formally tested whether, or how strongly, such disassortative mating behavior exists in house mice. It is certainly present in other species of *Mus*. I have found much better reproductive success in nonlittermate pairings of *M. cooki* and *M. pahari*. This reluctance to breed with littermates is nearly absolute in the vole *M. californicus* in the laboratory (R. Sage, observation). This behavior should be systematically investigated in house mice because of its importance in determining social structure in natural populations.

None of the *Mus* seem to require vegetable matter for reproduction, and they do well on a standard pelleted rat diet. To stimulate reluctant breeders I have supplementally fed them pure canary seed, which has been soaked in water for 24 hours. This is a technique sometimes used with granivorous finches to induce breeding activity. Whether or not this materially increased the rate of breeding in the wild mice I cannot say, but it certainly confirms the findings of Rowe *et al.* (1974) of the fondness that mice have for this seed. After only a couple of days of conditioning most of the animals come out of their nests and eagerly wait to eat the seed as it is dropped into the cage. It would not be surprising if there are special ingredients in the diet of wild mice that do promote the estrous cycle at the beginning of a normal spring breeding season, but the nutritional aspects of wild mouse biology have not been studied.

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NOTE ADDED IN PROOF

Since this chapter was submitted some important papers dealing with wild mouse biology have appeared. Schnell and Selander (1981) observed no correlation between enzymatic and morphological variability in Danish *M. musculus* and *M. domesticus*. A report on enzymatic variation in *M. domesticus* from Peru has appeared (Berry and Peters, 1981). Studies on *H-2* antigens of *M. domesticus* and *M. musculus* from Europe and North Africa revealed high levels of heterozygosity and confusing patterns of genetic similarity in animals from the native range (Götze *et al.*, 1980; Nadeau *et al.*, 1981). A 3-year population-cage study of wild *M. domesticus* by Van Zegeren (1980) tested for genetic changes in aggressiveness associated with changes in density levels. The results suggested that behavioral rather than genetic factors regulate density. Lloyd (1980) reviews the question of social behavior in the regulation of mouse populations.

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