

## **Social Structure of Feral House Mouse (*Mus musculus* L.) Populations: Effects of Resource Partitioning**

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**Summary.** 1. Social structure of house mouse (*Mus musculus* L.) populations in quarter-acre (0.1-ha) enclosures was organized differently with respect to centralized and decentralized food (corn) sites. Analysis of social structure indicated a well defined demic organization in populations containing a single, centralized food depot, whereas social structure in decentralized grids was more flexible.

2. A newly-derived dominance index, based on urinary marking patterns, indicated that social dominants were associated with food site location. Subordinate males were less likely to be trapped at food sites in centralized grids than were dominants; subordinate males were excluded to a lesser extent from food sites in decentralized grids.

3. Standard pairing experiments upon termination of the study substantiated that dominant males had significantly higher urinary marking patterns than subordinate males.

### **Introduction**

Numerous investigators have studied the regulation of population size in small mammals (e.g., Krebs 1964; McLaren 1971; Schaffer 1973; Krebs and Myers 1974; Flowerdew 1974). Behavioral interactions constitute an important means by which population density may be regulated (Calhoun 1949; Crowcroft and Rowe 1963; Wynne-Edwards 1965; McLaren 1971; Lloyd 1975; Stueck and Barrett 1978).

Social hierarchies have been proposed as a mechanism for partitioning the available food and space in the environment (Anderson and Hill 1965; Reimer and Petras 1967; Newsome 1969; Anderson 1970; Oakeshott 1974; Lloyd 1975; Krebs 1978). Consequently, resource partitioning may function as an important determinant for spatial distribution and sub-

sequent social interactions among members of the hierarchy (Brown 1953; Crowcroft 1955; Calhoun 1962; DeLong 1967; Anderson 1970). It is plausible that social behavior may operate as a suitable internal modulator to regulate feral house mouse population density (Calhoun 1952; Reimer and Petras 1967; Oakeshott 1974; Poole and Morgan 1976).

*Mus* populations are known to exhibit demic social structures, especially in confined laboratory or in barn populations (Reimer and Petras 1967; Anderson 1970; DeFries and McClearn 1972; Berry 1978; Butler 1980). Social dominance is thought to revolve around a dominant male with associated females and subordinate males (Mackintosh 1973; Oakeshott 1974). Myers (1974) offers contradictory evidence for field populations. Laboratory and field studies have shown that social relationships such as territoriality and competition are modified when resources such as food, cover, and/or nesting sites become limited (Strecker 1955; Southwick 1955; Crowcroft and Rowe 1963; Newsome 1969, 1970; Mackintosh 1970). Oakeshott (1974), however, suggested that such results may be magnified in laboratory studies and have limited relevance to natural populations. A major objective of our study was to evaluate these social parameters under natural field conditions.

For example, Christian (1970) postulated that socially subordinate animals dispersed from the source of competition. Thus, the development of social hierarchies facilitates dispersal of populations into spatially distinct breeding areas (Crowcroft 1955; Crowcroft and Rowe 1963; Anderson 1970; DeFries and McClearn 1970; Oakeshott 1974; Lloyd 1975).

Recent studies of scent marking in small mammals revealed the importance of social olfaction as a means of communication (Cheal and Sprott 1971; Johnson 1973; Stoddart 1974). Dominant males appear to have a distinct social advantage over subordinate members because they more frequently label their environment

with excretory products (Ralls 1971; Reynolds 1971; Desjardins et al. 1973; Macrides et al. 1975). Urinary marking appears to represent an important source of information for house mouse populations. The intensity and type of behavioral response is influenced by the concentration and content of pheromonal substance within the urine (Bronson and Caroom 1971; Jones and Nowell 1974; Maruniak et al. 1974; Macrides et al. 1975). These pheromonal substances may also alter the secretion of gonadotropic and steroidal hormones (Scott and Pfaff 1970; Bronson 1973; Maruniak et al. 1974; Bronson 1974; Maruniak et al. 1975). Bronson and Desjardins (1974) noted that urinary marking operates through time-distance dimensions to increase the versatility of social olfaction as a method of communication. Aversive reactions to male mouse urine are caused by androgen metabolite byproducts released in the urine on androgen-dependent tissue (Mackintosh and Grant 1966; Ropartz 1968; Bronson and Caroom 1971; Bronson and Desjardins 1974; Chipman and Albrecht 1974; Muggford 1974).

Desjardins et al. (1973) examined urinary patterns and social status of laboratory mice. Dominant male *Mus* exhibited a high frequency of urinary markings with patterns distributed over a large surface area. Subordinates urinated less frequently, usually near the corners of the filter paper. Most studies involving the ecological significance of urinary marking have been conducted in the laboratory. Mackintosh (1973) noted that *Mus* social structure in field situations has not been adequately explored.

The major objective of the present study was to analyze the social structure of feral house mouse populations in response to differential placement of food resources under natural field conditions. Dominance indices, based on urinary marking patterns, were used to evaluate feral *Mus* population structure in an attempt to understand better the effect of energy (food) location upon house mouse population regulation.

## Materials and Methods

Details concerning the field experimental design for the present investigation have been previously reported (Stueck and Barrett 1978). Only those materials and methods which relate directly to the investigation will be summarized.

**Study Area.** This study was conducted at the Ecology Research Center, Miami University, Oxford, Ohio. Feral *Mus* populations were restricted in 8 contiguous quarter-acre (0.1-ha) enclosures constructed with 20-gauge galvanized steel. Similar enclosures have been previously described (Barrett 1968; Suttman and Barrett 1979). Each enclosure was uniformly plowed, disked, fertilized (45.4 kg; 10-10-8, N-P-K), and seeded on 26 April 1975 with a mixture of grasses consisting of rye grass (*Secale* sp. -4.5 kg), fescue (*Festuca* sp. -6.8 kg), and Kentucky bluegrass (*Poa* sp.

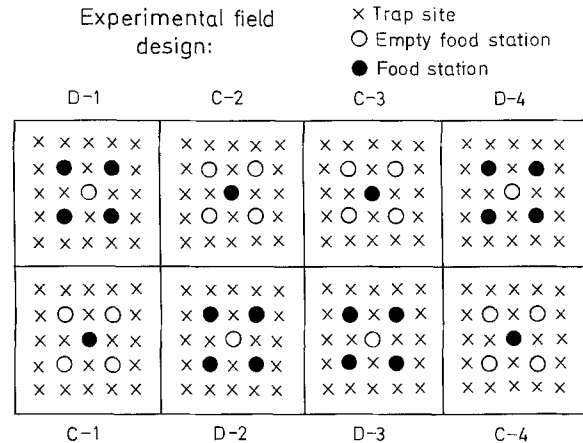


Fig. 1. Experimental design showing decentralized (D) and centralized (C) grids

-11.3 kg). Straw was uniformly scattered in each grid to aid seed germination and to provide ample cover during the initial part of the study. An area (60 cm) was mowed around the inside edge of each grid to prevent animals from escaping via tall vegetation next to enclosure walls. An electric fence surrounding the enclosures served to reduce predation (Barrett 1968).

Each grid contained five evenly-spaced feeding houses (Fig. 1). Ears of corn were used as the food source. Food placement was randomized, i.e., four quarter-acre (0.1-ha) plots were designated as centralized and four plots were designated as decentralized. Alternative seed sources were reduced by periodically hand-mowing the vegetation approximately 0.5 m above ground level (see Stueck and Barrett (1978) for details).

**Trapping Technique.** Feral house mice were obtained by live-trapping in local granaries during May and June, 1975. Each 0.1-ha grid was stocked on 6 June 1975 with 4 pairs of adult *Mus* randomized by weight and reproductive condition. Mice were marked by toe-clipping.

Traps were set in 5 columns and 5 rows at 6.1 m intervals in each grid (Fig. 1). Three additional traps were set around each food house to equalize the number of traps at food houses versus open field trapping sites. Thus, a total of 40 Sherman-type live-traps were employed per grid. Traps were baited with peanut butter. Trapping was conducted twice weekly. Population densities were estimated by the calendar-of-catches method (Petruzewicz and Andrzejewski 1962).

**Urinary Marking Methodology.** Scrotal males (>15 g) were used for urinary marking studies. Females were not used because additional handling stress of pregnant animals might adversely affect reproduction in the field.

Eight experimental chambers (46 × 46 × 76 cm) were constructed of 0.5 inch plywood. Thin mesh wire screen (0.1 gauge) was attached to the bottom to prevent filter paper destruction by the experimental animals. Hardware cloth served to prevent escape from the top of the chamber. Number 1 (46 × 46 cm) Whatman filter paper was placed under each chamber. The 8 chambers were separated by a distance of 30 cm. Each chamber was painted white to equalize experimental conditions. Possible olfactory interference was reduced by scrubbing each chamber with soap and water following testing. Tests were conducted under a photoperiod which corresponded to ambient conditions.

There was one test chamber to complement each field grid. Ideally, 8 male mice could be tested singly for each trapping date.

Traps were checked at 07.30 h and randomly-selected mice were transferred to the laboratory where each was allowed access to water ad libitum. Water bottles were removed after a 3-h acclimation period and a new sheet of filter paper was placed under the chamber for a 12-h (12.00–24.00-h) testing period. Mice were immediately returned to the field and released at the site of capture.

**Dominance Index Derivation.** Desjardins et al. (1973) demonstrated the importance of urinary marking density, area and distribution in relation to house mice rank. Filter paper containing the urine marks was illuminated by ultraviolet light and quantified as follows:

Density = number marks/filter paper.

This measure scored the total number of marks present on each sheet of filter paper for each animal tested.

Area = area (cm<sup>2</sup>) of marks/filter paper.

Urinary markings for each animal were traced on aluminum foil. The foil was then cut and individually weighed on a Mettler balance. A conversion factor was formulated by individually weighing three 1-cm<sup>2</sup> pieces of tin foil for each test run and converting the mean weight to cm<sup>2</sup>.

Frequency = number of ranked squares/plexiglass grid.

Distribution of marks for each animal was calculated by using a 46 cm × 46 cm plexiglass grid which was evenly divided into 100 (4.6 × 4.6 cm) squares. When placed over a filter paper sample, the number of squares containing at least 1 mark was scored and divided by 100 to provide the frequency value.

A dominance index was developed to incorporate the density, area, and frequency parameters. Importance values have long been employed in vegetation studies to rank plant species according to importance (Phillips 1959). Such a procedure was adopted for obtaining the relative dominance ranks of *Mus* in our study. Each sample (filter paper) was divided by the total measure of all samples to give relative density, area, and frequency. Thus, the urinary dominance index equals the relative density plus the relative marking area plus the relative marking frequency. Each animal was ranked in order of social dominance.

**Pairing Tests.** Pairing represents a direct method of ranking male house mice (Grant and Mackintosh 1963). Data were collected just prior to the termination of the study (December, 1975) for adult male mice. All individuals that had been previously scored for social dominance by the urinary marking technique were paired following a randomization procedure and ranked (Grant and Mackintosh 1963). Pairing data were then compared to urinary marking patterns, i.e., compared to the dominance index data for analysis.

## Results

### Dominance Index

The frequency distribution of urinary dominance values for field populations is presented in Fig. 2. Dominant and subordinate individuals exhibited different urinary marking patterns. There existed, however, an array of marking patterns (i.e., a gradient of dominance values) between dominant and subordinate individuals (Fig. 2). Thus, it was necessary to establish a break point in the distribution curves for dominant and subordinate animals. Dominance curves for centralized and decentralized grid popula-

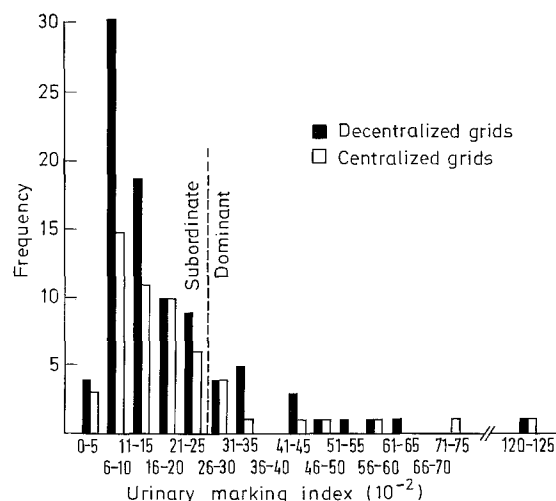


Fig. 2. Frequency distribution of dominance index values from male mice sampled from all field populations

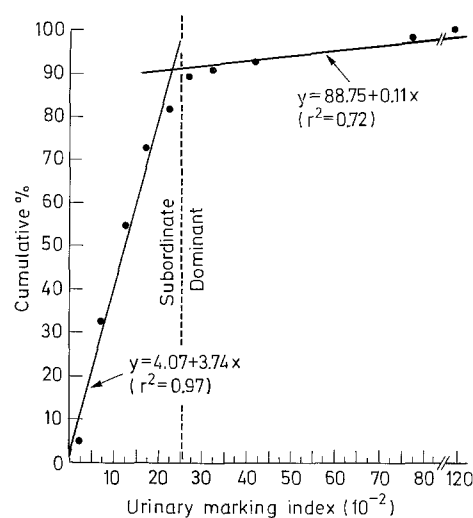
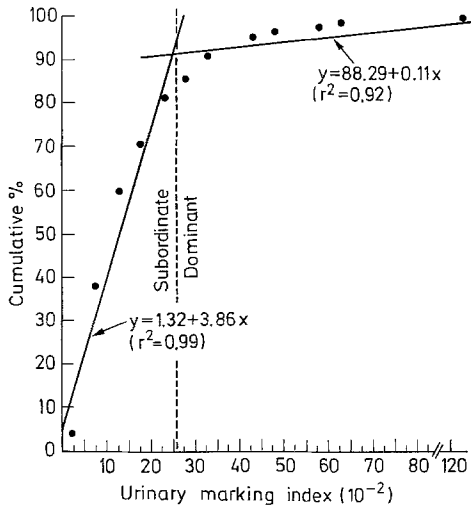


Fig. 3. Dominance index ranges and frequency of samples of decentralized grid populations plotted in terms of cumulative percentage. Cumulative percent was computed by plotting the percentage of values in the lowest dominance index range and expressing these data on a percentage basis. Dotted line derived from the intersection of lines regressed by least squares fit

tions are presented in Figs. 3 and 4, respectively. The break point for both grid populations was an index value of  $26 \times 10^{-2}$  (see Fig. 2). Dominance was considered to lie to the right of this value (i.e.,  $> 26 \times 10^{-2}$ ) and subordination to the left of this value (i.e.,  $< 26 \times 10^{-2}$ ). Components of the dominance index were found to have high correlation coefficients with these dominance index curves (density,  $r^2 = 0.90$ ; frequency,  $r^2 = 0.90$ ; area,  $r^2 = 0.63$ ). Area was the most variable because the total area of several small marks deposited by a dominant male may equal the



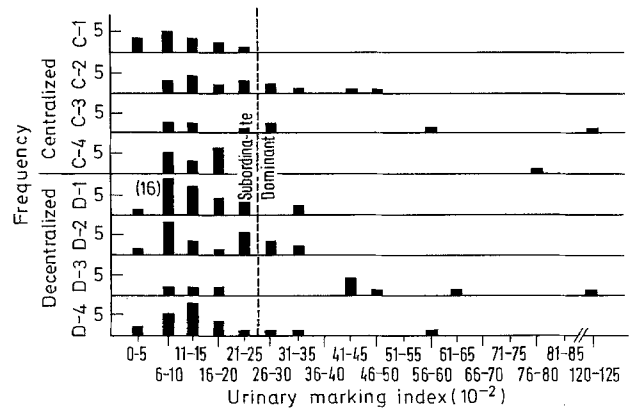
**Fig. 4.** Dominance index ranges and frequency of samples of centralized grid populations plotted in terms of cumulative percentage. Cumulative percent was computed by plotting the percentage of values in the lowest dominance index range and then by accumulating the number in each subsequent range and expressing these data on a percentage basis. *Dotted line* derived from the intersection of lines regressed by least squares fit

total area of a few large marks deposited by a subordinate animal.

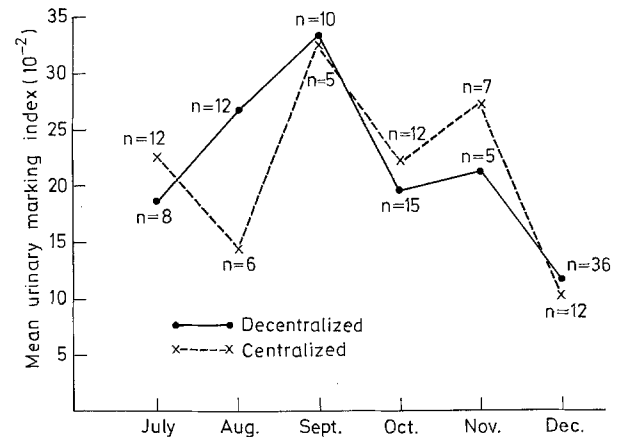
We hypothesized that a relationship existed between marking frequency and population density. Figure 5 compares mean dominance values for centralized and decentralized grid populations. Grids D-3 and C-3 had the lowest densities at carrying capacity with 16 and 23 animals/0.1 ha, respectively, and exhibited the widest and most uniform dominance distribution range.

No significant differences ( $P > 0.05$ ) were found between mean dominance values of centralized and decentralized populations. However, increased urinary marking values were evident in August for mice taken from both grid populations, after which time there was a sharp decline for both centralized and decentralized populations (Fig. 6). The change in urinary marking activity corresponded to increased population density trends. Stueck and Barrett (1978) showed that house mouse population densities increased sharply for both centralized and decentralized grids beginning in September and reached a peak in late October and early November. They also found that food resources at the feeding stations were utilized most during this time. The decreased mean dominance value in September may reflect a change in social structure as the population density increased towards peak numbers.

The social status of males trapped at food stations versus those trapped at non-food stations was compared for centralized and decentralized populations.



**Fig. 5.** Frequency distribution of samples falling in dominance index ranges for centralized and decentralized grid populations. *Dotted line* represents the dominance index break as determined in Figs. 4 and 5



**Fig. 6.** Mean dominance index values plotted through time

Juveniles (< 15 g) were included in this analysis because of their importance in increasing inter-male aggression as a result of crowding (Oakeshott 1974; Lloyd 1975). A dominance value  $\geq 26 \times 10^{-2}$  was used to distinguish dominant from subordinate individuals.

Dominant individuals within centralized populations were trapped with significantly higher frequency at food station sites as opposed to non-food station sites ( $t = 2.51$ ,  $P \leq 0.05$ ,  $df = 3$ ). Furthermore, there was a significantly higher frequency of subordinate males trapped at non-food stations in centralized grids ( $t = 2.77$ ,  $P \leq 0.05$ ,  $df = 3$ ). This suggests that the single food depot had a pronounced effect on the social structure of the dominant male population within centralized grids.

Although a food station may not have contained food, shelter and cover were available and, therefore, represented an advantage to those animals that were able to defend these 'resource' structures. Dominant

individuals were trapped at significantly higher frequencies at these 'resource' stations as compared to 'non-resource' trap sites (i.e., at trap sites in the open field; see Fig. 1) in centralized populations ( $t=2.49$ ,  $P\leq 0.05$ ,  $df=3$ ). Subordinate males were found to be present in significantly higher frequencies at 'non-resource' trap sites in centralized grids ( $t=4.17$ ,  $P\leq 0.01$ ,  $df=3$ ). No significant differences were found between trapping frequencies of dominant and subordinate males for 'resource' vs 'non-resource' sites in decentralized grids. Subordinate males in decentralized grids, however, were trapped with significantly greater frequency around 'resource' stations than were subordinate males from centralized populations ( $t=3.03$ ,  $P\leq 0.05$ ,  $df=3$ ). Thus, although dominant males were more likely to be the residents of the actual food site structures in both grid-types, subordinate males were apparently able to use (or forced to use) empty food stations as a resource (e.g., a shelter site) in decentralized grids.

### Pairing

Pairing data were collected prior to the termination of the study. The criterion used for determining rank was based on the degree of observable aggression towards opponents (e.g., biting, chasing, induction of a submissive posture). Ranking consequently resulted in 50% winners and 50% losers. Males were grouped according to previously determined individual urinary marking values (i.e., according to social dominances), paired for rank determination, then a second individual urinary marking test was conducted following pairing. Winners ( $\bar{X}=22$ ) marked approximately twice as much as losers ( $\bar{X}=10$ ). Furthermore, winners were found to have significantly higher dominance values than losers ( $t=3.32$ ,  $P\leq 0.01$ ,  $df=28$ ) both before and after pairing.

### Discussion

Population density has been found to be influenced by social dominance (Crowcroft 1955; Southwick 1955; DeLong 1967; Newsome 1969, 1970; Oakeshott 1974; Bronson 1973). We hypothesized that inhibition of scent marking by a small proportion of highly aggressive, despotic males would be indicative of territoriality within our study populations. Energy (corn) was available in equivalent amounts in each grid. The degree of social interaction was, therefore, dependent upon the food patterns (i.e., centralized versus decentralized grids). The resulting population densities of both grid-types were found to be determined by these food patterns (Stueck and Barrett 1978). For example, Stueck and Barrett (1978) found that

the mean peak density in the centralized grids was  $\approx 20$  animals per grid, whereas mean peak density in the decentralized grids was  $\approx 30$  animals per grid. We interpreted the increased dominance values in September (i.e., just prior to population density increase) as an indication of disruptive changes in population social structure.

Wilson (1975) described the concept of behavioral scaling which may be applicable to the urinary marking patterns manifested by populations in the present study. Territories are easily established and maintained during the initial stages of population increase but become difficult to defend with excessive numbers. The type of territorial system formed is dependent on the degree of environmental complexity and the abundance of resources (Lloyd 1975). Our findings tend to confirm these observations, especially concerning the pattern of food resources.

Newsome (1970) postulated that habitat features (e.g., runways and burrow holes) reduce excessive social interaction around a resource in demand. In this study, subsequent increased population density resulted in overcrowding which appeared to have been expressed through inhibition of pheromonal advertisement of subordinate members. The increased urinary marking values of centralized and decentralized populations, in September, prior to peak density, indicated increased competition for resources (e.g., feeding sites). Scent marking was inhibited during the peak densities in centralized and decentralized grids.

Defense of food sites by dominant males may be susceptible to disruption under high population density. Increased social stress may decrease reproductive success of females which, in the final analysis, will determine population size (Brown 1953; DeLong 1967; Lloyd and Christian 1969). Interestingly, Stueck (1976) found that prereproductive females from both grid-types had significantly increased adrenal weights as compared to adult females. This suggests that this segment of the population was under stress.

Trapping frequencies suggested that centralized grid populations exhibited a different social structure as compared to decentralized populations. There was no significant difference between the trapping frequency of dominant and subordinate males at food stations in decentralized grids. However, dominant males were most likely to be trapped at food stations in centralized grids. Thus, the single food depot in centralized grids had a pronounced effect on the location of dominant and subordinate males, i.e., food location appeared to cause a more rigid territoriality in centralized grid populations as compared to decentralized grid populations.

Populations are able to self-limit their numbers when a small number of males dominates the behav-

four of other members of the population (Crowcroft and Rowe 1963; DeLong 1967; Oakeshott 1974). We propose that this phenomenon was operative in centralized grids which had a mean population density of 20 animals in contrast to a mean density of 30 animals in decentralized grids. Social structures in centralized grids appeared to be organized in rigid social hierarchies as a result of the one food depot's causing a reduced carrying capacity (Stueck and Barrett 1978).

A significant finding was the verification of scent marking as a behavioral index for small mammal populations functioning under natural field conditions. Dominant males trapped from grid populations were found to mark with higher density ( $\bar{X}=22$ ) than subordinate males ( $\bar{X}=10$ ). They marked considerably less, however, than isolated laboratory mice (30–80 marks) reported by Desjardins et al. (1973).

In summary, the concept that population social structure consists of a series of demes controlled by a few dominant males was supported by both field and laboratory information. Our data suggest that (a) dominant males defended areas near food site structures, especially in centralized grids, and (b) centralized grid populations exhibited a more rigid social structure.

These findings illustrate the importance of habitat structure which may, in turn, significantly influence the social structure of natural populations. This study also illustrates the importance of integrating field and laboratory studies in order to ascertain the social structure of small mammal populations as they function as part of natural ecosystems.

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