Behavioural variation in wild house mice *Mus domesticus* Rutty: a quantitative assessment of female social organization

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Abstract. Female mice living in a high density enclosed population of 77–90 mice were classified into five social classes on the basis of their breeding status and spatial range. Activity, frequencies of interactions with males and with females, agonistic scores against males and against females and non-social behaviour were measured over a short period for each of 63 adults living together in the population. Multivariate discriminant function analysis discriminated four of the five female classes \((P < 0.0001)\) on the basis of interaction frequencies and agonistic scores, especially against other females, and the derived functions classified 94% of females into their correct pre-defined class. Territorial males were discriminated from non-territorial males \((P < 0.0001)\) by their greater activity, interaction frequencies and agonistic scores against other males, and the derived function classified 96% of males into their correct pre-defined class. Analysis of males and females together discriminated all classes except non-breeding females that had very restricted spatial ranges versus non-territorial males. Variation in reproductive success among individual females was related both to their social class and variation in the quality of their nest sites, and provides an explanation for the stability of high density mouse populations provided with excess food. Non-breeding females with access to the highest quality resources underwent few interactions with other mice; advantages for delaying reproduction in response to social cues which signal poor breeding conditions are discussed.

House mice living in favourable environments often maintain stable and persistent populations at very high densities due to density-dependent changes in rates of reproduction, juvenile survival and migration (Bronson 1979; Gliwicz 1980; Berry 1981). Reproduction decreases at high density due to delayed puberty in juvenile females, anoestrus or lengthened oestrous cycles in adult females, intra-uterine resorption and reduced litter sizes (see Bronson 1979; Pelikan 1981 for reviews), while nestling survival decreases due to increased nest disturbance, changes in maternal behaviour and cannibalism (Brown 1953; Southwick 1955; Rowe et al. 1964; Lloyd & Christian 1969; Lidicker 1976; DeLong 1978; Pennycuik et al. 1986). These changes are attributed to increased social stress in crowded populations (Lloyd & Christian 1969; Christian 1970; Lloyd 1975) and pheromonal cues present in mouse urine (Bronson & Coquelin 1980; Brown 1985). However, not all individuals are affected equally and some females continue to breed and rear their offspring, even at the highest densities (e.g. Lloyd & Christian 1969; Lidicker 1976).

Lomnicki (1978, 1980) presented a model that shows how individual variation in access to limited resources increases the stability of a population, as individuals which have access to insufficient resources cannot reproduce and may migrate from the reproductive population. Social status and habitat heterogeneity may be important sources of individual variation in resource access among house mice. The relationship between social organization and individual variation in reproductive success has been investigated among male house mice (Kuse & DeFries 1976; Baker 1981; Dewsbury 1982; Singleton & Hay 1983), and interaction between the territorial organization of males and habitat heterogeneity has significant effects on both the reproductive success of individual males (Wolff 1985) and the density of the entire population (Stueck & Barrett 1978; Noyes et al. 1982).

Comparatively little is known about the social organization of female mice, or the effects of resource heterogeneity on the reproductive success of individual females. However there is increasing...
recognition of the active role of females in mate choice (Doty 1974; D'Udine & Alleva 1983; Wolff 1985; Hurst 1986), and of the importance of variation in female behaviour in the evolution of reproductive strategies (Blaffer-Hrdy & Williams 1983). Most of the density-dependent pathways involved in population regulation outlined above act through changes in female behaviour and physiology, thus variation in these characteristics between the females when resources are limited will be crucial for individual reproductive success, and for the density and stability of the population as a whole.

Many studies report that females help to defend male territories, but potential differences between the females have not been examined (Crowcroft & Rowe 1963; Crowcroft 1966; Reimer & Petras 1967; Lidicker 1976; Butler 1980; Baker 1981; Singleton & Hay 1983). Lloyd (1975) found that breeding females in a dense captive population had wide spatial ranges often incorporating several male territories, while the movements of non-breeding females were very restricted, and individual reproductive success could apparently be related to a ranking based on activity and distances moved among females studied by Lloyd & Christian (1969). DeLong (1978) found similar differences between breeding and non-breeding females, but only very limited quantitative data have ever been presented. In any case, spatial ranges are difficult to compare either within or between populations as range depends largely on habitat structure (e.g. compare Reimer & Petras 1967; Lloyd 1975; Lidicker 1976).

During a study of a stable, high density population of house mice supplied with excess food and living in an enclosure in which high quality nest and food resources were unevenly distributed (Hurst 1984), female mice were classified according to their breeding status and spatial distribution. In this paper I present quantitative data that show highly significant differences in social behaviour between female classes, and multivariate discriminant function analyses provided a measure of these differences both within and between the sexes.

**METHODS**

**Mouse Population**

An enclosed population of house mice was established in March 1980, founded by four pairs of first generation wild-caught mice. The population was allowed to grow freely, with no further mice added before the end of this study in February 1982. The number of mice in the population had increased to a stable level of 77–90 mice before, and throughout, the main part of this study (Hurst 1984).

The mice were housed in a circular enclosure of 2.5 m diameter (5 m²), formed by a sheet of steel 60 cm high and marked with tape along the top edge at 24 equal intervals. In farm buildings where natural populations of mice are frequently dense, the building structure and contents provide extensive areas of cover and the main food, water and nest sites are generally separated in space. To simulate such an environment, two glass-topped nest boxes, one food pot and a single water source were provided to give four separate high quality resource areas (Fig. 1). A layer of shredded paper, 5–8 cm deep throughout the enclosure, provided cover and nesting material while still allowing a clear view of active mice. Partially covered mice remained in view, though mice stationary under deep litter could not be identified.

Pellet food, diet 41B (Heygate & Sons) and water were provided ad libitum. Food was always placed within the food pot, but mice carried single pellets around the enclosure. All mice did not therefore have to visit the food pot but could eat pellets removed by other mice. The enclosure was kept under reverse day lighting conditions, with dim red lighting during the day supplemented by white light from 2100 to 0900 hours. The temperature was kept at 22–26°C, and mice were subjected to only the minimum disturbance. The enclosure was cleaned out every 6 weeks, renewing the shredded paper but leaving any nests containing pups.

Unmarked mice weighing more than 10 g were given unique and permanent freeze marks which allowed identification of all adult mice at a distance of up to 3 m (Hurst, in press). With extensive practice, involving reference to written and photographic records, mice could be recognized at a glance, usually from any part of their mark pattern.

**Social Structure**

The mice were observed frequently between March 1980 and February 1982 (5–40 h per week). Observations included mapping the movements and behaviour of individual mice, recording the identities, locations and behaviour of interacting
Figure 1. Spatial distributions of adult mice over the 6-week study period, and location of nest boxes (1, 2), food pot (F) and water spout (W). Dashed lines indicate approximate borders of the eight male territories, though there were minor variations during the study. Non-territorial males and Non-breeding Restricted females lived within and between the dominance territories (TD). Unrestricted females (classes BU, NU) spent most of their time in the shaded area, while hatched areas indicate ranges of Breeding Restricted females (BR) and females with partial access to high quality resources (BP). Social classes are described in Table I.

mice, and recording the presence and behaviour of mice within particular areas. Variation in behaviour between males corresponded to social classes previously described in the literature (Table I). At any one time there were eight–nine territorial males each defending a small area of the enclosure for up to 7 months. Females were generally more difficult to separate into distinct categories but could be separated into five classes on the basis of their spatial restrictions and involvement in breeding (Table I). Some females operated in small areas of the enclosure like males, but many were much less restricted to one area and spent most of their time around the nest box and food resources (Fig. 1). Only certain females were seen to mate and/or became visibly pregnant, although most of the females were perforate. In contrast to Lloyd & Christian (1969) and Lloyd (1975) breeding status was not related simply to differences in spatial range. Although mice with very restricted ranges were not involved in breeding (Non-breeding Restricted females) neither were Non-breeding Unrestricted females that ranged over several male territories (Table I, Fig. 1; see also Singleton & Hay 1983). Pups were born within the nest boxes and within nests built around the enclosure. Only juveniles reared within the nest boxes survived to independence, presumably because the boxes provided physical protection from social disturbance (Crowcroft & Rowe 1957, 1958).

Individual Behaviour

During 10-min observation periods, the identities of all active mice were recorded, together with their behaviour and location in the enclosure. Active mice were defined as mice moving around the enclosure, or mice that were stationary for only part of the observation period. Mice remaining in one location throughout an observation period, or making very short movements between resting sites, were not regarded as ‘active’ and were not recorded. The majority of mice were identified during the first few minutes of a period, and identities were confirmed and changes in behaviour recorded during the remainder of the period. All types of behaviour were recorded following definitions in Grant & Mackintosh (1963) and Mackintosh (1981), but particular attention was paid to the infrequent social interactions so that all interactions involving active mice were recorded. Previous observations of individual mice in the enclosure showed that only 5.4% of time was spent in behaviour associated with agonism, reproduction, or social investigation (Hurst 1984). Interactions which involved sequences of many elements were summarized as single interactions, for example Mate with X, Fight X, Attack and Chase X, Investigate X, so that each interaction between two mice was recorded only once.

Observation periods were spread between 0600 and 2400 hours to allow for temporal variation in the activity of individual mice and of the population as a whole. Ninety-six periods were recorded over the 12-h dark phase of the light:dark cycle, using random numbers to select each start time to the nearest minute. Recording commenced when an electronic beeper set to a 60-s interval sounded into an earpiece. Similarly, an additional eight periods were selected and recorded between 0600 and 0900 hours and eight periods between 2100 and 2400 hours to allow for any mice that were active only in the light (see, for example, Crowcroft 1966).
Hurst: Social organization among female house mice

Table I. Social classes of mice observed in the enclosure

<table>
<thead>
<tr>
<th>Name</th>
<th>Acronym</th>
<th>Description</th>
</tr>
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<tbody>
<tr>
<td>Males</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Exclusive territorial</td>
<td>TX</td>
<td>Defended territories with the exclusion of all other males and some females. Mated with females. Previously described by Crowcroft 1955, 1966; Crowcroft &amp; Rowe 1963; Poole &amp; Morgan 1976</td>
</tr>
<tr>
<td>Dominance territorial</td>
<td>TD</td>
<td>Defended an area against other males, particularly excluding other territorial males. Some subdominant and subordinate males tolerated, though encounters frequently led to the attack and pursuit of SD, and attack of SO males. Mated with females. Previously described by Reimer &amp; Petras 1967; Mackintosh 1970; Poole &amp; Morgan 1976</td>
</tr>
<tr>
<td>Subdominant</td>
<td>SD</td>
<td>Lived within dominance territories, sometimes contributing to defence, and often invaded other territories. Attacked by females in invaded and home territories, but were generally in good condition with few bite scars. Sometimes rested in huddles with other mice but were frequently found alone. Never seen mating, though attempted to mount females. Previously described by Crowcroft 1966; Evans &amp; Mackintosh 1976; Poole &amp; Morgan 1976</td>
</tr>
<tr>
<td>Subordinate</td>
<td>SO</td>
<td>Lived within dominance territories but movements were more limited than SD and they were usually found in a huddle with other mice. They were of medium to poor physical condition, judging from bite scars and fur loss. Largely non-aggressive, but there was some mutual fighting. Never seen mating. Previously described by all authors given above</td>
</tr>
<tr>
<td>Young adult subordinate</td>
<td>SY</td>
<td>Spent most of their active time in resource areas, despite being attacked and chased by resident males and females (sometimes tolerated by females). In excellent physical condition but never seen mating. Behaviour similar to older offspring described by Crowcroft 1966</td>
</tr>
<tr>
<td>Females</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Breeding, unrestricted access to resources*</td>
<td>BU</td>
<td>Moved freely between nest boxes and food pot, and some were highly mobile around the enclosure. They defended resources against invading males and females, and were the only females that attacked resident territorial males. They often mated with more than one territorial male, sometimes on the same day</td>
</tr>
<tr>
<td>Breeding, restricted access to resources*</td>
<td>BR</td>
<td>Lived in, and helped defend, single male territories that were not based around the food pot, water or nest boxes, and had little spatial overlap with other females. Mated only with the resident territory male and offspring never reared to independence</td>
</tr>
<tr>
<td>Breeding, partial access to resources*</td>
<td>BP</td>
<td>Spent much of their time around one of the nest boxes (Fig. 1) though they mated with neighbouring territorial males and were attacked by the resident male. They were chased from other resource areas by the resident males and females</td>
</tr>
<tr>
<td>Non-breeding, unrestricted access to resources*</td>
<td>NU</td>
<td>Similar distributions to BU females though tended to be less mobile. Never seen mating, pregnant, or lactating</td>
</tr>
<tr>
<td>Non-breeding, restricted access to resources*</td>
<td>NR</td>
<td>Chased from resource areas by resident males and females, though some were rarely seen away from the huddles formed with subordinate males. Never seen mating, pregnant, or lactating</td>
</tr>
</tbody>
</table>

* Resources = food pot, water, or nest boxes.

The 112 observation periods were spread over 6 weeks (15–23 per week), with at least 30 min between observation periods recorded on the same day. As individual mice in the population were active for a maximum of 18 min, it was unlikely that mice active in one period remained active until
the next. No adult mice died over the 6-week period and all mice adult before the first observation period were marked (35 females and 28 males).

**Data Analysis**

All 63 adult mice were active in at least 10 observation periods and up to 34 mice were active during any one period (mode = 24). The number of mice active per period was independent of the hour of day and there was no evidence of individuals or discrete groups of mice active at different times (Hurst 1984). Each individual was classified according to Table I on the basis of its behaviour during the observation periods, supplemented by further observations made during the 6 weeks (60 h approximately). No mice appeared to change social class during this period. A total of 705 interactions were recorded during observation periods, with a maximum of 11 interactions in any one 10-min period. Both interacting mice were identified in 427 interactions (60·6%). There were only 25 cases in which an individual mouse was involved in more than one interaction during a single observation period, and only three of these cases involved more than one interaction between the same dyad of mice. As observation periods were well separated in time and no one mouse was active in more than 71% of observation periods (median = 31%), it was assumed that the interactions were independent. The expected frequencies of interaction between particular dyads of mice were calculated from the number of observation periods in which both members of a dyad were active (i.e. available to interact), multiplied by the proportion of all active dyads that resulted in an interaction.

Agonistic interactions were transformed into agonistic scores for each mouse by assigning a differential score to each type of agonistic interaction: interactions that involved attacks and chases by one or both mice scored 5, threatening behaviour only without physical contact (Threat, Rattle, Circle, Zigzag; see Mackintosh 1981) or jumping on another mouse without a biting attack scored 3, scuffles over food or unpursued flight scored 2. The scores of each individual were totalled for all periods, with each aggressive role given a positive score and each non-aggressive role given a negative score. Both participants in a Fight, where both played an aggressive role, were given positive scores (+5). Six behavioural measures were then calculated for each mouse: (1) number of observation periods in which the mouse was active (Activity), transformed to \( \log_{10} \) (Activity) to normalize the data; (2) frequency of interactions with males per active period (MInt); (3) frequency of interactions with females per active period (FInt); (4) agonistic score in interactions with males per active period (MAg); (5) agonistic score in interactions with females per active period (FAg); (6) frequency of eating, drinking and exploring per active period (Non-social).

Univariate F-ratios were calculated to examine differences between social classes for each behaviour measure. Multivariate canonical discriminant function analyses (SPSS) were then used to examine the relative importance of the six measures in discriminating between the pre-defined social classes, and to examine the relative distances between classes on this basis. There was very little correlation between the behaviours, the largest pooled within-groups correlation being -0·34 between frequencies of interactions with females and agonistic scores against females. Discriminant analyses carried out on the five female social classes, and on the five male classes, derived sets of functions that maximized variation in behaviour between the classes relative to variation within classes. To select optimal subsets of the behaviours that maximized separation of the classes, behaviours were entered stepwise into each analysis according to the MAXMINF criterion, selecting successive behaviours that maximized the smallest F-ratio between any one pair of classes. Only those behaviours with a partial F-ratio of \( P < 0·5 \) and which accounted for at least 0·1% of the within-class variance were included. The magnitude of the derived function coefficients and within-group correlation coefficients indicated the importance of each behaviour in the separation of classes (see Gittins 1985).

Classes that were not significantly separated (\( P > 0·05 \)) in the first analysis were combined and a new set of functions was derived for the reduced number of classes. Finally, a discriminant analysis was carried out on male and female classes together to examine the relative distances between all social classes in the population.

**RESULTS**

There were more interactions between two males and fewer between two females than predicted from
their dyadic activity ($\chi^2 = 13.4$, df = 2, $P < 0.05$), though there was no difference in activity between individual males and females ($t = 0.087$, ns); 60.3% of the interactions were agonistic. Taking into account the unequal numbers of males and females, males were both aggressive and subjected to aggression more often than females ($\chi^2 = 32.7$ and 41.9, $P < 0.001$ respectively). The behaviour of mice in each social class is summarized in Fig. 2 and differences between the classes are examined below.

**Discrimination between Female Classes**

There were significant differences ($P < 0.001$) between female classes for all behaviours except non-social behaviour ($F = 1.70$, df = 4.30, $P < 0.18$). Multivariate discriminant function analysis provided significant separation ($P < 0.01$) between all paired combinations of the five female classes except Breeding Unrestricted versus Breeding Restricted ($F = 0.801$, df = 4.27, $P < 0.54$) and Breeding Unrestricted versus Non-breeding Unrestricted ($F = 1.87$, df = 4.27, $P < 0.14$). As there was almost no difference between Breeding Unrestricted and Breeding Restricted females these two classes were combined (BU/R females).

Subsequent discriminant analysis provided clear separation ($P < 0.0001$) of all pairs of the four female classes (Fig. 3) and classified 33 of the 35 females into their correct pre-defined social class. Activity and non-social behaviour did not contribute to this discrimination, and the first two of the three derived functions accounted for virtually all of the total variance in the other four behaviours (Table II). Agonistic scores against other females and interaction frequencies with other females were
Table II. Discriminant analysis between four classes of females (BU/R, BP, NU, NR): standardized function coefficients, within-group correlation coefficients (in parentheses), and significance of partial F-ratios for behaviours contributing to the discrimination.

<table>
<thead>
<tr>
<th>% Variance</th>
<th>Canonical correlation</th>
<th>MInt</th>
<th>Flnt</th>
<th>MAg</th>
<th>FAg</th>
<th>Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Function 1</td>
<td>75.18</td>
<td>0.935*</td>
<td>-0.665</td>
<td>-0.606</td>
<td>0.520</td>
<td>0.798</td>
</tr>
<tr>
<td>Function 2</td>
<td>24.81</td>
<td>0.833*</td>
<td>0.488</td>
<td>0.685</td>
<td>0.472</td>
<td>0.655</td>
</tr>
<tr>
<td>Significance of partial F</td>
<td>0.001</td>
<td>0.000</td>
<td>0.010</td>
<td>0.000</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

MInt, Flnt: interaction frequencies with males or females; MAg, FAg: agonistic scores against males or females.

† Social classes are described in Table I.

‡ Non-social behaviour and Activity made no contribution to the discrimination.

* P < 0.0001.

Figure 4. Discriminant analysis of the five male classes (see Table I): plots of discriminant scores for the first two of three derived functions. A significant proportion of the variance in male behaviour was accounted for (Wilks’ $L = 0.147$, $P < 0.0001$). Function 1 accounted for 92.4% of this variance, with a canonical correlation of 0.895. There was no significant separation of TX versus TD ($F = 1.01$, $df = 3.21$, $P < 0.41$), SD versus SO ($F = 2.32$, $df = 3.21$, $P < 0.11$), or SO versus SY ($F = 1.68$, $df = 3.21$, $P < 0.21$).

Discrimination between Male Classes

Discriminant analysis of all five male classes separated the two territorial classes from the three non-territorial classes but there was much overlap within these groups (Fig. 4). Classes were thus combined into territorial and non-territorial for all subsequent analyses. The mean scores of territorial males were significantly greater ($P < 0.001$) than of non-territorial males for all behaviours except non-social behaviour, which was more frequent among non-territorial males ($F = 5.77$, $df = 1.26$, $P < 0.02$), and there was no significant difference in their agonistic scores against females ($F = 2.82$, $df = 1.26$, $P < 0.21$). In addition, the territorial males were responsible for all but one of the 28 mating sequences recorded during the observation periods.

Discriminant analysis produced a single function which accounted for a very significant proportion of the variance in behaviour between territorial and non-territorial males (Wilks’ $L = 0.274$, $P < 0.0001$) and classified all but one of the males correctly. Frequency of interactions with males, activity,
frequency of interactions with females and agonistic scores against males were of decreasing order of importance to the discrimination (Table III). In contrast to the discrimination of females, agonistic scores were only of minor importance because interactions were complicated by the territorial organization of the males. Males aggressive in their own territory, for example, usually fled from attack when invading another defended territory.

**Discrimination between Males and Females**

Discriminant analysis of the four female and two male classes together provided significant separation between all pairs of classes at *P* < 0.0001, except territorial males versus breeding (BU/R) females and non-territorial males versus Non-breeding Unrestricted females which were separated at *P* < 0.01, and non-territorial males versus Non-breeding Restricted females which were not separated significantly (*F* = 2.03, *df* = 5,53, *P* < 0.09). The last comparison reflected the similar lifestyles of non-territorial males and Non-breeding Restricted females which lived in the same area of the enclosure (see Fig. 1, Table I).

Only non-social behaviour made no contribution to the analysis and the first two of five derived functions accounted for 97.4% of the total variance in the other behaviours (Table IV). These functions classified 76.2% of the mice into their correct predefined classes, and Fig. 5 shows the relative distances between female and male classes. Function 1 again contrasted high interaction frequencies with low agonistic scores, and widely separated the breeding females with partial access to resources from all other mice (BP in Fig. 5). These females were the only mice in the population that interacted frequently and had very low agonistic scores, due to attacks from other residents around the nest box where they spent most of their time (see Fig. 1). Function 2 gave positive weight to all behaviour scores, especially agonistic scores against females.
Figure 5. Discriminant analysis of male (territorial, non-territorial) and female (BU/R, BP, NU, NR) classes (see Table I): plots of discriminant scores for the two significant derived functions (Table IV). The analysis accounted for a very significant proportion of the variance in behaviour (Wilks' $L = 0.073, P < 0.0001$). See text and Table IV for an interpretation of the function axes.

and this function discriminated territorial males and breeding (BU/R) females from all other mice.

The frequencies of interactions between the main classes of mice are summarized in Fig. 6, taking into account the dyadic activity of the mice. This figure emphasizes the very low frequencies of interactions involving non-breeding females, and only non-breeding females interacted with other mice in proportion to their dyadic activity. Breeding females were more likely to interact with territorial males or with other breeding females while they were active than with mice in other classes.

DISCUSSION

In common with other studies of captive mouse populations (Crowcroft & Rowe 1958, 1963; Reimer & Petras 1967; Singleton & Hay 1983) the frequency of agonistic interactions involving females was low in comparison with those between two males, but agonistic interactions were nevertheless important variables discriminating between female social classes. Similar female aggression has been observed directly in free-living populations (Anderson 1961; Hurst 1984, 1986), while the low incidence of bite scars on trapped females confirms that females are attacked less frequently than males (Southwick 1958; Rowe et al. 1964, 1983). Female aggression has been related to pregnancy and lactation (Crowcroft & Rowe 1963; St John & Corning 1973; Lidicker 1976; Lynds 1976; Singleton & Hay 1983) and should thus be a characteristic of breeding females, though caged groups of virgin females also attack strange female intruders (Ropartz & Haug 1975). It was not clear whether aggression in the present study was due entirely to the pregnant or lactating status of females, but some breeding females were consistently aggressive throughout the 6-week period, and females partially restricted from high quality resources became pregnant but did not attack the other mice. Aggression against other females may have been predetermined by prenatal exposure to androgens, as found among isolated laboratory females (vom Saal 1983), though aggressive females were also aggressive against males, which was not found in the laboratory tests, and they also had higher frequencies of social interactions than the other female classes.
Differences in interaction frequencies and agonistic scores between classes reflected major differences in reproductive status and use of space among both the female and male mice. Among males, reproduction is largely confined to those defending territories or dominant in agonistic interactions over a wide range of conditions (Crowcroft 1966; Reimer & Petras 1967; DeFries & McClearn 1972; Lloyd 1975; Kuse & DeFries 1976; Singleton & Hay 1983; present study). The defended territories provided areas in which territorial males and breeding females mated without disturbance from other mice, and I have observed similar defence of mating space by free-living male and female mice (Hurst 1986). In the enclosure, defended areas also contained nesting sites and juvenile survival depended on the protection of these sites from disturbance by other mice (see also Southwick 1955; Crowcroft & Rowe 1957, 1958; Rowe et al. 1964). The high frequencies of interactions shown by all breeding mice gave them the opportunity to monitor the presence and status of other mice using the same and neighbouring areas. Their aggression towards intruders decreased the density of mice in their mating and nesting space and thus probably increased their chances of successful reproduction.

Non-breeding status was clearly not maintained by social stress resulting from high levels of interactions (see Fig. 6), especially among females living in high quality resource areas. Breeding status may have been controlled through indirect social cues such as those present in mouse urine (reviewed by Brown 1985), though maintaining a non-breeding status must increase the fitness of the respondent for such cues to evolve. The ability to stay in a top quality habitat and delay reproduction would be an advantage for females with a low probability of raising their offspring, avoiding the risks and energy expenditure involved in reproduction or migration (Lidicker 1975; Horn & Rubenstein 1984), especially if conditions are likely to improve in the near future through a reduction in local density or increase in social status. In addition to any changes in reproductive physiology (Bronson 1979), non-breeding females minimized their risks from interactions with the other mice and did not contribute to defence, even of high quality resource areas. Breeding and non-breeding females which share nest sites are likely to be very closely related (e.g. Pennycuik et al. 1986); additional benefits of reproductive suppression for certain females under these circumstances are discussed by Brown (1985). However, although non-breeding females may have increased the fitness of their kin by delaying their own reproduction, they still contributed to the crowding of nest sites and they did not help to protect their kin from intruders. Their behaviour thus appears to be better adapted for maximizing their own long-term fitness.

This study showed that there were clear and quantifiable differences in the social behaviour of individual females related to their reproductive status, as suggested by previous studies of dense mouse populations. Such individual variation is likely to have important effects on the density and stability of these populations. Little is known about variation in behaviour within free-living populations, or changes in status of individuals through time. Long-term studies of individual behaviour and life histories are essential if we are to understand the significance of social organization in mouse populations.

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