# Rice plant damage distribution and home range distribution of the ricefield rat *Rattus argentiventer* (*Rodentia : Muridae*)

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ABSTRACT. The patterns of rice plant damage distribution and the home distribution of the ricefield rat *Rattus argentiventer* were studied in a two hectare experimental field and in a two hectare enclosure. Damaged rice plants were randomly (Poisson) distributed during the vegetative stage of rice plant growth but tended to be aggregated or contiguous during the generative stage. Analysis of the spatial distribution of the rats' home ranges, using MORISITA's index of dispersion and nearest neighbor distances, indicated that (i) males showed a slightly stronger tendency to congregate than females, and (ii) females showed a uniform distribution pattern and had mutually exclusive home ranges from the birth season through the lactation period. Before and after the birth season, female rats had a random distribution pattern. Furthermore, an analysis of the degree of home-range overlap between the sexes found that male and female home ranges were distributed almost independently during the non-breeding and early mating seasons. However, early in the breeding season and at the end of the mating season, male and female home ranges overlapped completely. Male and female home ranges were completely exclusive from pregnancy until the end of lactation.

KEY WORDS : Ricefield rat *Rattus argentiventer*, home range, distribution pattern, growth stage of rice plant, rat damage.

## INTRODUCTION

Rats can cause substantial economic loss in rice and most other crops, including palm oil, sugar cane, maize, cassava, soybean, groundnut, coconut, mung bean, and sweet potato. The current conservative estimate is that typically between 5 and 15% of the rice crop in rice-growing regions is lost because of rodents (Geddes, 1992).

In Southeast Asia, the reported impact of rodents is highest in Indonesia, where approximately 17% of rice production is lost to the ricefield rat (GEDDES, 1992).

In West Java, especially at the Jatisari field study site, the dominant species of small mammal in rice fields is *Rattus argentiventer* (ROBINSON & KLOSS, 1916). In their five-year study at various locations throughout Indonesia, MURAKAMI et al. (1990) reported that *R. argentiventer*

dominated samples of small mammals in rice fields. Less than one percent of the small mammals found were *Bandicota indica* (BECHSTEIN, 1800) or *Rattus rattus diardii* (JENTINK, 1879).

Several authors have discussed the general biology of the ricefield rat (LAM, 1983), and its breeding and control (HARRISON, 1951; BUCKLE et al., 1985; LAM, 1983; SINGLETON, 1997; SOEKARNO et al., 1978). TRISTIANI (1999) examined ricefield rat population parameters, especially birth and immigration, as well as the relationship between rat reproduction and the stages of growth of the rice plant (TRISTIANI et al., 1998). However, little is known of the behavior of this species in relation to population demography. Specifically, there has been little research to clearly reveal the relationship between spatial patterns of damage distribution, the rats' home range distribution, and the stages of growth of the rice plant.

Damage to rice plants by rats is by far the greatest agricultural problem in Indonesia (GEDDES, 1992; SINGLETON, 1997). An understanding of the rats' population dynamics,

habitat use and distribution pattern, and of the factors that influence their breeding, survival, and movement, is essential for developing an effective, economic, and sustainable management program (FIEDLER & FALL, 1996; SINGLETON & PETCH, 1994; SINGLETON, 1997).

An interesting aspect of the spatial pattern of damage distribution and the home range distribution is the effect on rat sampling and control strategies. A quantitative description of spatial pattern is essential, not only to understand the spatial or dispersion dynamics of populations, but also to develop appropriate sampling strategies for population surveys (IWAO, 1977). We examined the behavior of ricefield rat populations, focusing on rat damage from feeding and on individuals' home ranges, and on the relationship between the rats' reproduction and the growth stages of the rice plant.

The study had two objectives: 1) To determine the pattern of distribution of rat damage. 2) To examine changes in the home-range pattern with the stage of growth of the rice plant, in both a two-hectare experimental field and in a two-hectare enclosure. This information is essential in deciding how far apart poisoned bait should be placed, how to develop better farm management practices, and how to assess the likely transmission rates of potential biological control agents.

## MATERIAL AND METHODS

This study was carried out in a 2 ha experimental field, and in an enclosed 2 ha ricefield. The two sites were used to enable us to study the effect of migration on the rats' distribution pattern. In the experimental field, immigration and birth were the major factors in the growth of the rat population (TRISTIANI, 1999), whereas migration could not affect the rat population in the enclosed field. The field work was conducted from 1988 to 1990 at the Jatisari Forecasting Center in West Java, about 120 km east of Jakarta. The Center is an agricultural research station, and rice is the main crop grown.

Surrounding the enclosed field is a permanent concrete wall embedded into the ground to a depth of 0.6 m. On this is a wire-mesh fence 0.6 m high, topped with a second 0.4 m zinc fence. In addition, a 0.2 m zinc barrier was placed along both sides of the fence, at a vertical angle of 45º to effectively prevent any possibility of emigration or immigration. The effectiveness of this barrier was tested with an intensive capture-recapture survey, conducted both inside and outside the enclosure. The results showed that there was no rat migration into or out of the enclosed area.

The enclosure and the experimental field were cultivated during the December to May rainy season, and again during the June to October dry season. The field was left fallow in November. The rats in the enclosure were exterminated by trapping intensively for about one month until there was no evidence of bait being consumed

by rats. The enclosure was then deemed rat-free. Two weeks after transplanting the rice in the1989 rainy season, which started in December 1988, thirty adult male and thirty adult female rats were released in the enclosure. All the rats used in the experiment were individually marked with a combination of toe and ear clips. Once the maximum population was reached at the end of each season, the non-tagged rats were removed from the enclosure to prevent severe rat damage to the ricefield.

Single capture live-traps made of wire mesh (200 x 110 x 110 mm: 100 mm$^2$ mesh) were used to conduct a census of the rat population. The traps were placed in the 10 x 10 m sections of a large grid (110 x 180 m). Each trap was baited with whole grain, which was wrapped with cotton mesh and suspended from the center of the trap. This is a proven method for live-trapping this species (MURAKAMI et al., 1990). For five days, the traps were set at about 5:30 p.m. and then checked the next morning. All of the traps were then removed for a ten-day period. This cycle was maintained throughout the study, meaning that trapping was conducted twice monthly.

Each morning, all the captured rats were transported to a processing station. Rats caught for the first time were marked with a combination of toe and ear clips. The rats were counted, weighed, sexed, and examined externally to determine their reproductive condition. They were then released before sunset, at about 5:30 p.m., at their respective capture sites.

Rats were classified as adult males ($\geq$110 g), adult females ($\geq$60 g), sub-adult males (40-109 g), sub-adult females (40-59 g) or juveniles ($\leq$40 g).

### Monitoring rat damage

The study area was a ricefield that was already divided into experimental and enclosed fields. There were 10800 rice plant hills in the enclosure and 7200 hills in the experimental field, at regular intervals of 0.25 m, each with three rice seedlings, transplanted together.

Rice plants were sampled randomly on different days and from different hills. Damaged tillers were recorded and counted. The location of each damaged plant was marked with a bamboo cane and color-coded tape that indicated when it was damaged. The spatial pattern of damage was analyzed statistically by examining the frequency distribution of damaged tillers per sampling unit.

Six plots (10 by 10 m) were sampled in the experimental field, and nine plots (10 by 10 m) were sampled in the enclosure. Each plot contained 1200 hills. Observations were conducted three weeks after the ricefield was transplanted, in the maximum tillering stage, during panicle primordia initiation, and in the booting, flowering, milky, and ripening stages. The phenology of the rice plant is briefly reviewed in Appendix 1.

## Spatial distribution pattern of rat damage

To interpret the general pattern of rat damage at each stage of rice plant growth, the overall distribution of the damage was analyzed. Earlier studies of spatial point patterns were primarily concerned with comparing area (or quadrate) counts to a Poisson distribution; departures indicate that the pattern is not completely spatially random (CRESSIE, 1993). Furthermore, CRESSIE (1993) stated that the degree of departure is usually measured by an index based on the quadrate count (e.g., FISHER et al., 1922; DAVID & MOORE, 1954; MORISITA, 1959; LLOYD, 1967).

We tested the goodness of fit of the spatial distribution of rat damage to (1) the Poisson distribution, (2) the negative binomial distribution, and (3) IWAO's patchiness regression (IWAO, 1968).

### Goodness of fit of the Poisson distribution

The test for the goodness of fit of the Poisson distribution used the test statistic $x^2 = ss/\bar{x}$ with n-1 degree of freedom or $x^2 = ss/\mu$ with $\mu = n$, if $\mu$ is known (ZAR, 1999). To determine whether the distribution of each developmental stage departed from random, the number of damaged tillers per sampling unit was examined in terms of the variance-mean ratio. The null hypothesis in Poisson goodness of fit testing is one of random distribution of entities in space or time (ZAR, 1999). Furthermore ZAR (1999) stated that rejection of the hypothesis of randomness might result from one of two situations. First, the population distribution may be uniform; that is, each unit of space (or time) has the same number of entities. Second, the population may be arranged in what is referred to as a clustered, aggregated, or contiguous, distribution. If a population has a random distribution, $\sigma^2 = \mu$ and $\sigma^2/\mu = 1.0$. If the population distribution is more uniform than random (sometimes called "underdispersed"), $\sigma^2 < \mu$ and $\sigma^2/\mu < 1.0$. If a population is distributed contiguously (sometimes termed "overdispersed"), $\sigma^2 > \mu$ and $\sigma^2/\mu > 1.0$. The departure of the rat damage distribution pattern from randomness (Poisson distribution) was tested by calculating the index of dispersal, $I$, for every sampling as

$$I = \frac{s^2}{\bar{x}}$$

where $s^2$ represents variance and  represents mean of damaged tillers.

### Fit to the negative binomial distribution

The mathematical distribution that is sometimes used to describe contiguous distributions of biological data is the negative binomial distribution (ZAR, 1999). The negative binomial distribution has two parameters: (1) $\bar{x}$, the mean number of individuals per sampling unit or the mean number of damaged tillers per sampling unit and (2) $k$, a parameter related to the degree of clumping (LUDWING &

REYNOLDS, 1988). The goodness of fit of the rat damage distribution for each stage of rice development was examined using ANSCOMBE's statistic T (ANSCOMBE, 1950):

$$T = \frac{1}{n} \sum_{i=1}^{n} (x_i - \bar{x})^3 - s^2 \left( \frac{2s^2}{\bar{x}} - 1 \right)$$

where $n$ is the number of sampling unit, $x_i$ is the number of damaged tillers in the $i$th sample unit, and $\bar{x}$ represents the mean number of damaged tillers. The value of $T$ was compared with its standard error:

$$S.E.(T) = \sqrt{\frac{2\bar{x}(k+1)\frac{\bar{x}^2}{k^2}\left(1+\frac{\bar{x}}{k}\right)^2\left\{2\left(3+5\frac{\bar{x}}{k}\right)+3k\left(1-\frac{\bar{x}}{k}\right)\right\}}{n}}$$

where $k = \dfrac{\bar{x}^2}{s^2 - \bar{x}}$.

$T/S.E.(T)$ should lie between $\pm 1.96$ if the negative binomial distribution is a satisfactory model.

### IWAO's patchiness regression

In LLOYD's (1967) "mean crowding", $\overset{*}{x}$, indicates the average number of events sharing a quadrate with an arbitrary event, and is calculated as:

$$\overset{*}{x} = \bar{x} + \left( \frac{s^2}{\bar{x}} - 1 \right)$$

where $\bar{x}$ represents the mean number of damaged tillers and $s^2$ represents variance. IWAO (1968) found that LLOYD's (1967) mean crowding is linearly related with the mean density over a range of different densities in a wide variety of situations, including both theoretical and biological distribution. The relationship is shown by

$$\overset{*}{x} = \alpha + \beta \bar{x},$$

where $\alpha$ is the intercept on the $\overset{*}{x}$-axis and $\beta$ is the regression coefficient. The index of basic contiguity, $\alpha$, is the number of other damaged tillers in the same sampling unit. The index $\beta$ (the density-contiguity coefficient) is a measure of the distribution of rat damage, and takes values of $<1$, $=1$, and $>1$ for uniform, random and aggregated distribution, respectively (IWAO & KUNO, 1971). Furthermore, IWAO & KUNO (1971) showed that estimation of $\alpha$ and $\beta$ for a set of distributions can be made by the usual least squares method, and the fitness to the linear regression may conveniently be indicated by the coefficient of determination, $r^2$ (r: correlation coefficient).

### Spatial distribution of home range

The area of each individual's home range was determined by a modification of the minimum-convex-polygon method (MARES & LACHER, 1987). The distribution of the trap stations at which a given number of different individuals (i.e., 0, 1, 2, or 3 separate rats) were recorded during each survey period was examined. It was assumed that a given rat could be caught in all traps within its home range, even though in practice some were not caught in all of the stations within their home range. Juveniles were

excluded from this analysis, because they may continue to remain within their mothers' home ranges (MURAKAMI, unpublished observations). The dispersion pattern was assessed using MORISITA's index of dispersion, $I_B$, index (MORISITA, 1962), calculated as:

$$I_B = I_\delta \frac{n}{n-1}$$

$$\text{with } I_\delta = \frac{n\sum_{i=1}^{n} x_i(x_i - 1)}{n\bar{x}(n\bar{x} - 1)}$$

where $n$ is the total number of observations and $x_i$ is the number of individuals in the $i$th quadrate.

The degree of spatial correlation or the degree of home range overlap relative to an independent distribution was determined using IWAO's $\omega$-index (IWAO, 1977). The value of $\omega$ changes from its minimum of -1 for complete exclusion, through 0 for independent occurrence, to the maximum of +1 for complete overlapping.

## RESULTS

### Distribution pattern of rat damage

During the rice plants' vegetative growth stage, the variance-mean ratio never exceeded the critical value of $p=0.05$,

for a random distribution. During the generative stage, however, the variance-mean ratio always exceeded the critical value of $p=0.05$. Fig. 1 summarizes the goodness of fit to a random distribution. The relation of $s^2/\bar{x}$ to $\bar{x}$ in Fig. 1 indicates that the variance-mean ratio increased linearly with the mean in every generative stage, and almost always exceeded unity. It is obvious from Fig. 1 that the variance-mean ratio during the generative stage departs from randomness.

If spatial randomness (sr) during the generative stage is rejected, the next step in a spatial analysis is to measure the departure from sr. Table 1 summarizes the goodness of fit to the negative binomial model for all the observed data during the generative stage. The results show that the value of $T/S.E.(T)$ for each stage during the generative stage of rice plants lies between ±1.96 or the value of $T$ is always smaller than the standard error. The results show that during the rice plants' generative growth stage, the distribution of rat damage followed the negative binomial distribution.

Analysis of the goodness of fit of IWAO's patchiness regression showed that the values of $\alpha$ (index of basic contiguity) and $\beta$ (the density-contiguity coefficient) are $\alpha \cong 0$ and $\beta \cong 1$ during the rice plants' vegetative growth stage (Table 2). This indicates that the distribution of rat damage was approximately random during the vegetative stage. However, during the generative stage (from panicle initiation to ripening) the patterns changed to $\alpha > 1$ and $\alpha > 1$, indicating aggregated or contiguous distribution.

TABLE 1

Summary of the goodness of fit of the rat damage distribution to the negative binomial distribution for all rice plant stages, calculated by ANSCOMBE's T-statistic. S.E. is standard error (S.E.) of T.

| Stage of rice plant | 1989 dry season T ± S.E | 1989 rainy season T ± S.E | 1990 dry season T ± S.E | 1990 rainy season T ± S.E |
|---|---|---|---|---|
| *Enclosure* | | | | |
| panicle initation | 0.15 ± 19.05 | 3.84 ± 17.96 | 3.76 ± 12.79 | 7.47 ± 17.20 |
| booting | -0.63 ± 8.70 | 0.74 ± 6.98 | -1.43 ± 7.08 | 0.58 ± 13.26 |
| flowering | -0.99 ± 7.12 | 0.27 ± 7.17 | 7.11 ± 13.45 | 7.47 ± 17.20 |
| milky | 6.31 ± 7.10 | 5.34 ± 13.31 | 0.29 ± 0.32 | 0.09 ± 0.26 |
| ripening | -0.03 ± 7.28 | 12.25 ± 13.31 | 0.98 ± 1.67 | -0.47 ± 0.50 |
| *Experimental field* | | | | |
| panicle initation | -0.27 ± 2.82 | 2.91 ± 14.98 | 0.44 ± 1.08 | 1.77 ± 6.27 |
| booting | 5.95 ± 11.51 | 3.74 ± 16.08 | -1.71 ± 2.85 | 0.98 ± 9.26 |
| flowering | -0.56 ± 2.78 | 0.31 ± 12.01 | 4.68 ± 21.91 | 9.89 ± 16.78 |
| milky | 5.52 ± 8.10 | 3.54 ± 16.13 | 1.44 ± 2.08 | 0.77 ± 5.23 |
| ripening | -0.74 ± 11.52 | 8.24 ± 10.31 | 0.57 ± 1.69 | -1.16 ± 6.30 |



Fig. 1. – Relation of the variance-mean ratio to the mean in enclosure (A) and experimental field (B). The broken line is the critical value at $p=0.05$ for random distribution. Black circles indicate vegetative stage rice plants, white circles indicate generative stage. $s^2$ represents variance and $\bar{x}$ represents mean number of damaged tillers.
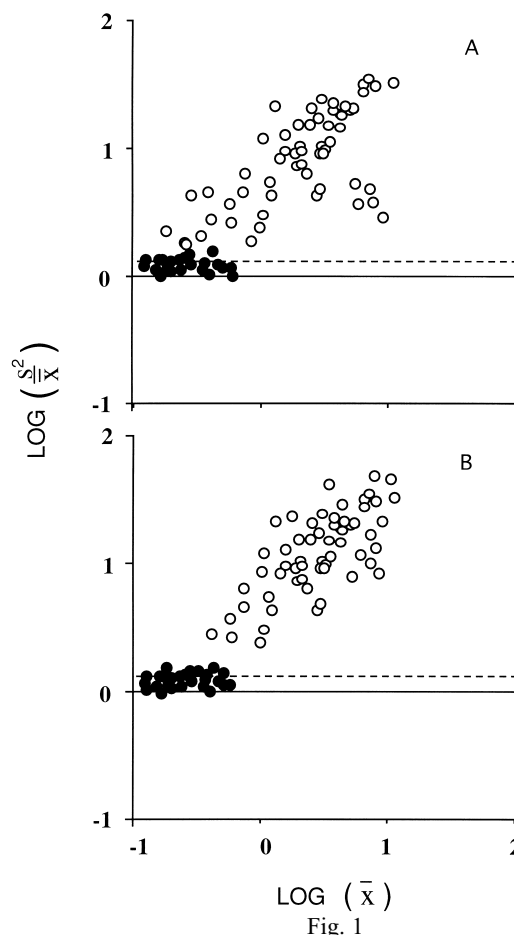
TABLE 2

Statistics of IWAO's patchiness regression (mean crowding vs. mean) for the different growth stages of rice plants in both the enclosed and experimental fields. The value of $\alpha$ represents the index of basic contiguity and $\beta$ is the density-contiguity coefficient. $r^2$ represents the coefficient of determination (r: correlation coefficient).

| Stage of Rice plant | | Enclosure | | | Experimental field | | |
|---|---|---|---|---|---|---|---|
| | | $\alpha$ | $\beta$ | $r^2$ | $\alpha$ | $\beta$ | $r^2$ |
| *1989-dry season* | | | | | | | |
| Tillering | $\alpha \cong 0$ | 0.028 | 1.021 | 0.882 | 0.015 | 0.823 | 0.862 |
| Max.tillering | $\beta \cong 1$ | -0.096 | 1.085 | 0.948 | -0.086 | 1.045 | 0.914 |
| Panicle initation | | 2.078 | 7.576 | 0.879 | 7.018 | 1.536 | 0.909 |
| Booting | $\alpha > 1$ | 1.385 | 8.941 | 0.965 | 7.988 | 2.042 | 0.912 |
| Flowering | $\beta > 1$ | 1.439 | 7.831 | 0.951 | 7.193 | 1.431 | 0.941 |
| Milky | | 1.614 | 6.607 | 0.819 | 1.114 | 6.206 | 0.839 |
| Ripening | | 1.578 | 6.897 | 0.828 | 2.272 | 3.417 | 0.923 |
| *1989-rainy season* | | | | | | | |
| Tillering | $\alpha \cong 0$ | -0.058 | 0.777 | 0.828 | -0.047 | 0.731 | 0.891 |
| Max.tillering | $\beta \cong 1$ | -0.046 | 0.972 | 0.816 | -0.041 | 0.911 | 0.848 |
| Panicle initation | | 6.696 | 2.424 | 0.998 | 7.162 | 1.624 | 0.944 |
| Booting | $\alpha > 1$ | 8.581 | 1.874 | 0.912 | 8.089 | 1.984 | 0.931 |
| Flowering | $\beta > 1$ | 6.947 | 1.523 | 0.806 | 7.218 | 1.622 | 0.902 |
| Milky | | 7.487 | 6.777 | 0.968 | 7.061 | 6.422 | 0.898 |
| Ripening | | 7.107 | 6.972 | 0.957 | 7.114 | 6.611 | 0.899 |
| 1990-dry season | | | | | | | |
| Tillering | $\alpha \cong 0$ | 0.016 | 0.832 | 0.874 | 0.019 | 0.933 | 0.901 |
| Max.tillering | $\beta \cong 1$ | -0.077 | 1.032 | 0.974 | -0.069 | 1.011 | 0.899 |
| Panicle initation | | 7.249 | 1.623 | 0.951 | 7.157 | 1.824 | 0.934 |
| Booting | | 8.106 | 2.398 | 0.941 | 7.989 | 2.197 | 0.954 |
| Flowering | $\alpha > 1$ | 7.547 | 1.524 | 0.993 | 7.441 | 1.403 | 0.925 |
| Milky | $\beta > 1$ | 1.182 | 6.467 | 0.841 | 1.197 | 6.263 | 0.867 |
| Ripening | | 2.359 | 3.731 | 0.969 | 1.999 | 3.086 | 0.918 |
| *1990-rainy season* | | | | | | | |
| Tillering | $\alpha \cong 0$ | 0.014 | 0.955 | 0.931 | 0.016 | 0.842 | 0.827 |
| Max.tillering | $\beta \cong 1$ | 0.025 | 0.773 | 0.888 | 0.021 | 0.699 | 0.899 |
| Panicle initation | | 7.545 | 1.985 | 0.952 | 7.023 | 1.976 | 0.945 |
| Booting | | 7.219 | 1.656 | 0.914 | 7.112 | 1.656 | 0.914 |
| Flowering | $\alpha > 1$ | 6.545 | 1.985 | 0.952 | 6.545 | 1.875 | 0.915 |
| Milky | $\beta > 1$ | 7.219 | 2.656 | 0.814 | 7.107 | 2.214 | 0.902 |
| Ripening | | 0.258 | 6.648 | 0.984 | 0.301 | 3.041 | 0.912 |

## Home range distribution pattern

The patterns of dispersion for male and female rats were analyzed separately for the two fields (Table 3). In terms of the $I_B$-index, males had a slightly stronger tendency to congregate than females. For most females, the $I_B$-index was approximately zero from early-March to early-May and from early-August to early-October. From the birth season through the lactation period, females showed a uniform pattern of distribution and their home ranges tended to be mutually exclusive. They had a random distribution pattern before and after the birth season.

The $\omega$-index was used to examine the degree that the home ranges of the sexes overlapped in each survey period.

The results show that at the peak of the birth seasons, from March to mid April and from August to mid September, the lack of home-range overlap between males and females amounted to almost complete exclusion (most of the $\omega$-indices approximately equal to -1, Table 4). However, during the early mating seasons (early-January and early-June) and non-breeding season (November and December) most of the $\omega$-indices were less than $0.5 \cong 0$, indicating that the degree of home-range overlap between males and females was an independent occurrence. From the end of the mating season until the pregnancy (February and July) and lactating periods (May and October), most of the $\omega$-indices were approximately equal to +1, indicating that male and female home ranges completely overlapped.

TABLE 3

Summary of home range distributions in the enclosure and in the experimental field calculated by the value of the $I_B$-index.
I and II refer to the first and second survey periods for each month, respectively. M, male; F, female.

| | | Jan I | Jan II | Feb I | Feb II | Mar I | Mar II | Apr I | Apr II | May I | May II | Jun I | Jun II | Jul I | Jul II | Aug I | Aug II | Sep I | Sep II | Oct I | Oct II | Nov I | Nov II | Dec I | Dec II |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Enclosure** | | | | | | *(birth season)* | | *(birth season)* | | | | | | | | | | | | | | | | | |
| 1989 | M | 1.71 | 2.02 | 2.31 | 2.22 | 4.21 | 4.14 | 5.48 | 2.12 | 2.33 | 1.59 | 2.29 | 2.52 | 2.71 | 7.38 | 5.10 | 4.16 | 6.28 | 5.95 | 4.15 | 2.41 | 1.58 | 1.38 | 1.84 | 1.85 |
| $I_B$-index | F | 0.61 | 0.99 | 0.53 | 0.71 | 0.08 | 0.07 | 0.09 | 0.04 | 0.06 | 0.72 | 0.70 | 0.64 | 0.50 | 0.54 | 0.07 | 0.05 | 0.08 | 0.03 | 0.09 | 0.82 | 0.59 | 0.81 | 0.50 | 0.90 |
| 1990 | M | 1.51 | 2.41 | 1.72 | 2.51 | 2.30 | 4.12 | 3.22 | 1.22 | 1.52 | 1.53 | 2.51 | 3.23 | 2.82 | 6.03 | 4.98 | 4.26 | 3.96 | 4.14 | 5.51 | 2.14 | 1.76 | 2.57 | 1.46 | 1.94 |
| $I_B$-index | F | 0.76 | 0.85 | 0.58 | 0.73 | 0.06 | 0.09 | 0.04 | 0.02 | 0.09 | 0.81 | 0.74 | 0.81 | 0.61 | 0.52 | 0.06 | 0.08 | 0.05 | 0.02 | 0.06 | 0.57 | 0.54 | 0.63 | 0.58 | 0.86 |
| **Experimental field** | | | | | | | | | | | | | | | | *(birth season)* | | | | | | | | | |
| 1989 | M | 2.53 | 2.51 | 3.89 | 2.99 | 3.72 | 3.21 | 5.83 | 6.70 | 2.60 | 3.57 | 3.08 | 4.07 | 3.08 | 6.40 | 4.10 | 4.49 | 2.51 | 5.18 | 3.88 | 4.94 | 3.80 | 1.50 | 2.86 | 1.65 |
| $I_B$-index | F | 1.31 | 1.20 | 1.36 | 0.62 | 0.06 | 0.03 | 0.04 | 0.02 | 0.08 | 0.23 | 2.90 | 2.80 | 0.14 | 0.61 | 0.04 | 0.09 | 0.03 | 0.18 | 0.08 | 0.80 | 0.70 | 0.50 | 0.53 | 1.01 |
| 1990 | M | 2.70 | 1.98 | 1.80 | 1.91 | 3.20 | 3.13 | 3.47 | 4.11 | 4.32 | 5.38 | 6.28 | 6.51 | 2.70 | 4.37 | 5.09 | 4.15. | 4.27 | 5.94 | 5.14 | 6.40 | 4.37 | 4.37 | 2.83 | 2.83 |
| $I_B$-index | F | 1.30 | 1.38 | 1.10 | 0.89 | 0.08 | 0.07 | 0.09 | 0.08 | 0.09 | 0.42 | 1.40 | 1.50 | 1.46 | 0.59 | 0.07 | 0.10 | 0.09 | 0.07 | 0.05 | 0.82 | 1.76 | 1.70 | 0.59 | 0.96 |

TABLE 4

Summary of the degree of home-range overlap between the sexes in the enclosure and in the experimental field, calculated by the value of the ω-index.
I and II refer to the first and second survey periods for each month, respectively. M, male; F, female.

| | Jan I | Jan II | Feb I | Feb II | Mar I | Mar II | Apr I | Apr II | May I | May II | Jun I | Jun II | Jul I | Jul II | Aug I | Aug II | Sep I | Sep II | Oct I | Oct II | Nov I | Nov II | Dec I | Dec II |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Enclosure (M and F)** ω | | | | | *(birth season)* | | | | | | | | | | | | | | | | | | | |
| 1989 | 0.58 | 0.59 | 0.84 | 0.97 | -0.87 | -0.79 | -0.60 | 0.81 | 0.83 | 0.49 | 0.41 | 0.78 | 0.96 | 0.91 | -0.82 | -0.90 | -0.99 | 0.97 | 0.73 | 0.89 | 0.28 | 0.21 | 0.11 | 0.14 |
| 1990 | 0.44 | 0.61 | 0.71 | 0.97 | -0.76 | -0.82 | 0.87 | 0.96 | 0.87 | 0.72 | 0.43 | 0.60 | 0.81 | 0.92 | -0.89 | -1.04 | -0.96 | 0.79 | 0.74 | 0.71 | 0.26 | 0.25 | 0.08 | 0.12 |
| **Experimental field** | | | | | | | | | | | | | | | *(birth season)* | | | | | | | | | |
| 1989 | 0.39 | 0.68 | 0.57 | 1.21 | -1.22 | -0.89 | -1.03 | 0.99 | 0.89 | 1.02 | 0.44 | 0.96 | 1.09 | 1.07 | -0.93 | -1.05 | -1.31 | 0.98 | 1.05 | 0.96 | 0.15 | 0.34 | 0.42 | 0.35 |
| 1990 | 0.48 | 0.69 | 0.84 | 1.01 | -1.04 | -0.99 | -1.02 | -1.06 | 0.99 | 0.86 | 0.39 | 1.01 | 0.99 | 1.02 | -0.97 | -1.00 | -0.98 | 0.42 | 0.89 | 0.82 | 0.47 | 0.35 | 0.01 | 0.09 |

## DISCUSSION

During the vegetative stage (from the tillering stage to the maximum tillering stage), rat damage was randomly distributed. However, during the generative stage it generally tended to be aggregated or contiguous. As pointed out by many authors, both plants and animals are seldom distributed at random (IWAO & KUNO, 1971). Among the species of animals and plants showing aggregated distribution patterns (LUDWING & REYNOLDS, 1988, IWAO & KUNO, 1971), three major types can be distinguished by the combination of $\alpha$ and $\beta$: (1) $\alpha > 0$ and $\beta \cong 1$; (2) $\alpha \cong 0$ and $\beta > 1$; and (3) $\alpha > 0$ and $\beta > 1$ (IWAO & KUNO, 1971). The distribution of ricefield rat damage belongs to type (3). IWAO & KUNO (1971) stated that type (3) seems to be the most common among animals and plants, as many organisms tend to be distributed in colonies or clumps. This is both because of their characteristic modes of reproduction and dispersal, and because they respond to the heterogeneous conditions of their habitat. The aggregation that occurs during the generative stage of rice plant growth might be due to heterogeneous conditions in the rats' habitat and/or rat behavioral factors.

There were no significant differences in the distribution patterns of the ricefield rat for the rainy and dry seasons. It is difficult to draw any definite conclusions from this result, since data are only available for four consecutive seasons. Long-term studies are needed to provide more detailed information on the influence of season on the distribution of rat damage.

The present study revealed that males have a stronger tendency to congregate (i.e., a larger $I_B$ value) than females, which seems to result from the male tendency to gather around females. Thus, some males were successful in approaching females, while others apparently were not. Interestingly, females showed a tendency toward under-dispersion or uniform distribution, suggesting that females achieve higher reproductive success by not congregating. The $I_B$ value of females tended to be zero during the birth season, indicating that the home ranges of females tended to be mutually exclusive. During this period, females may become more aggressive to establish territories and compete for resources. Among small mammals, reproductively active females generally maintain individual territories during the breeding season, which they actively defend from other females (BATZLI, 1985; REICH & TAMARIN, 1980). ANDERSON (1989) stated that females are unlikely to have to compete for copulation. Instead, the fitness of resident females may be limited by competition for territories that will provide the nutritional resources required for gestation and lactation, along with secure nest sites. Females' nutritional requirements are greatest during gestation and lactation (SADLEIR et al., 1973).

The degree of home-range overlap between the sexes was similar in both years. Our results indicate that during the non-breeding and early mating seasons, male and female home ranges were distributed almost independently. However, at the end of the mating season and early in the breeding season, male and female home ranges overlapped completely. From pregnancy until the end of lactation, male and female home ranges were completely exclusive. ANDERSON (1989) reported that resident males compete for females, while females compete for nutritional resources, nest sites, or for whatever parental investment is permitted in the mating system. This study also found that the home range of reproductively active adult females tended to be mutually exclusive during the breeding season. Female home ranges are more commonly exclusive of same-sex breeding residents than are those of males (JANNETT, 1980; MADISON, 1980a, 1980b; REICH & TAMARIN, 1980, 1984). During this period, the home ranges of adult males were almost completely independent. OSTFELDS (1985) argued that male territoriality is dependent on female strategy, and that male behavior should be territorial when female ranges are mutually overlapping, and non-territorial when female ranges are mutually exclusive. Adult males have been found to occupy home ranges that overlap those of females, but not those of other adult males, in marmots (ARMITAGE, 1974), house mice (FITZGERALD et al., 1981), woodrats (MACMILLEN, 1964), and voles (JANNETT, 1980, 1981; WOLFF, 1980). Our study shows that there was extensive home-range overlap between males and females during the breeding season, as well as considerable intrasexual home-range overlap between neighboring males. In summary, our study demonstrates the importance of considering temporal habitat use when interpreting spatial patterns of rat damage distribution and the home-range distribution of the ricefield rat.

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## APPENDIX 1

### Phenology of the rice plant (TRISTIANI et al. 1998).

The IR64 variety of rice takes about 113 days from germination to harvest and there are no significant differences in its developmental periods during the dry or wet seasons. The development is usually divided into two main categories: the growing or vegetative stage and the generative stage. The first stage (vegetative stage) lasts approximately one and half months and is characterized by: 1) germination period (±21-25 days), from when the seeds are sowed until plants are seedlings in the nursery; 2) tillering stage (±30-35 days), from when the seedlings are transplanted into the field; the number of seedlings planted per hill varies depending on the size and soil quantity of the field; 3) maximum tillering stage (±5-7 days), when the tillers per hill have developed. The generative stage lasts approximately two months and is characterized by five developmental events: 1) initiation of the panicle primordia (±7-10 days), when the bulb of the rice plant initially develops; 2) the booting stage (±10-14 days), when maximum bulb and stalk growth take place; 3) the flowering stage (±7-12 days), when flowers appear; 4) the milky stage (±5-8 days), when seeds form in a milky liquid; and, finally, 5) the ripening stage (±7-10 days), when the seeds ripen for harvest