Large epidemics of Japanese encephalitis during the 1960s in southwestern Japan

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Abstract: Based on statistical data from 22 prefectures in southwestern Japan, the relationships of the incidence of Japanese encephalitis (JE) to the density of swine farms and the area of paddy fields were analyzed, especially in relation to cattle-breeding farms during the 1960s. Large epidemics of JE often occurred in prefectures in which the total density of cattle and horse breeding farms was markedly above the density of swine farms, even when the density of swine farms was low and the area of paddy fields was less-developed. In prefectures in which the total density of cattle and horse breeding farms was relatively low, the incidence of JE correlated with the density of swine farms only in prefectures with fully-developed paddy fields. The reasons for these differences among the prefectures are discussed.

key words: Japanese encephalitis, Culex tritaeniorhynchus, host preference, anti-mosquito behaviour, density-dependent dispersion

INTRODUCTION

Recent decrease in the population of Culex tritaeniorhynchus, which resulted in fewer epidemics of Japanese encephalitis (JE), has been suggested to be partly caused by decreases in the number of livestock breeding farms and rice paddy field area (Kamimura and Matsuda, 1972; Nakamura, 1988; Nakamura et al., 1992ab). In the 1970s when a decrease in epidemics was observed, the incidence of JE was higher in prefectures showing a large number of swine-breeding farms per kilometer in prefectures with extensive paddy fields. However, the incidence of JE was not associated with the total number of cattle- or swine-breeding farms (Nakamura, 1988). Cattle are considered to play a small role as amplifying animals for the JE virus (Oya, 1967; Otsuka et al., 1969; Mitsuda et al., 1969; Bundo et al., 1983). The major differences in the state of livestock breeding between the 1960s and the 1970s included the lesser degree of mechanization and the very large number of farms breeding cattle, especially beef cattle, compared with swine-breeding farms in the 1960s. Did the large epidemics in the 1960s occur only due to a larger paddy field area and a higher number of swine-breeding farms in this period than in the 1970s?

Cx. tarsalis and Cx. nigripalpus, vectors of western equine encephalitis virus and St. Louis encephalitis virus, show seasonal changes in host preferences (Tempelis, 1970; Tempelis et al., 1967; Edman and Taylor, 1968). Host preference shifts from birds, which develop viremia after

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infection with these viruses and are preferred by mosquitoes that are insensitive to these viruses and are not initially preferred. This is because adequate feeding on birds which develop anti-mosquito behaviour becomes difficult when the population of mosquitoes increases to a certain level. Therefore, mosquitoes begin to feed on mammals that had fewer anti-mosquito behaviours (Edman and Kale, 1971; Edman et al., 1972, 1974; Kale et al., 1972; Webler and Edman, 1972). This shift in host preference decreases the population of infected mosquitoes but increases the probability of humans and horses being bitten by mosquitoes (Reeves, 1971).

*Cx. tritaeniorhynchus* prefers cattle to swine (Barnett, 1960; Mitchell et al., 1973; Reuben et al., 1992). The feeding rate on this species in barns decreases with increases in the number of collected mosquitoes. The degree of this decrease is more marked in cattle than in swine. In cattle, feeding becomes difficult at lower collection numbers. This may be because cattle are more sensitive than swine to mosquitoes (Fujito et al., 1971). These findings on other types of encephalitis such as western equine encephalitis suggest that it is not appropriate to exclude the role of cattle in JE epidemics. Therefore, based on statistical data we classified prefectures into those showing a very large number of cattle-breeding farms compared with swine and those showing a relatively small number of cattle-breeding farms, and evaluated the relationship between the density of swine-breeding farms and the incidence of JE in west Japan in the 1960s compared with that in the 1970s.

**MATERIALS AND METHODS**

The prefectures and data evaluated were the same as those in a previous study of the relationship between the state of livestock breeding and the incidence of JE in the 1970s (Nakamura, 1988). All prefectures in Kyushu, Shikoku, and Chugoku as well as Hyogo, Kyoto, Shiga, Mie, Wakayama, and Osaka prefecture were analyzed (total, 22 prefectures). Only these 22 prefectures in west Japan were selected for analysis because areas showing a high incidence of JE have been limited to west Japan since the 1960s compared with the 1950s (Miura, 1967; Oya, 1979). Data on the planted acreage of paddy fields and the number of farmers breeding dairy cattle, beef cattle, swine and horses were obtained from the World Census of Agriculture and Forestry and Statistical Yearbook for 1960, 1970, and 1980. Since the number of municipalities differed between 1960 and 1980 due to merging, the number in 1980 was used as the standard. Thus, the number of municipalities was the same as that in the previous study in the 1970s (Nakamura, 1988). Data were analyzed using the same number of municipalities as units in each period.

Data on the number of patients were based on the statistics of communicable disease and food poisoning, Japan, 1978 (Statistics and Information Department, Ministers’s Secretariat, Ministry of Health and Welfare).

In the 22 prefectures, the mean incidences (incidences) from 1960 to 1970 and those from 1970 to 1980 were calculated and used as the incidences in the 1960s and 1970s, respectively. In each prefecture, the paddy field ratio (ratio of the planted area to the entire area) was calculated using municipalities as units. In addition, the ratio of the number of municipalities showing 15.0%...
or more paddy fields to the total number of municipalities was calculated in 1960, 1970, and 1980. The mean value in 1960 and 1970 was used as the value in the 1960s and that in 1970 and 1980 as the value in the 1970s.

In each municipality showing 15.0% or more paddy fields, the number of livestock breeding farms per krf was obtained. The mean number in such municipalities was calculated according to prefectures in 1960 and 1970, and the mean value in both years was used as the mean barn density in the 1960s. Similarly, the mean barn density in the 1970s was calculated. In addition, such values were calculated for dairy cattle, beef cattle, swine, and horses. The sum value for dairy and beef cattle was defined as the cowshed density, the value for swine as the piggery density, and that for horses as the stable density. The sum of these densities was defined as the barn density. We used the density of animal farms not the number of animals as a parameter in this analysis. This was because the most basic factor associated with the number of patients in an area is whether a transmission cycle (mosquito - swine - mosquito) is established in that area. In other words, in the entire prefecture, the number of patients seems to be more markedly associated with the number of swine breeding farms, where a transmission cycle can be established, than the number of animals.

**RESULT**

Is there a relationship between the piggery density and the incidence of JE in the 1960s as was obtained in the 1970s?

As previously reported, in the 1970s, the incidence of JE was higher with a higher piggery density only in 9 prefectures where 20.0% or more municipalities showed 15.0% or more paddy fields (20.4-64.0%) (Nakamura, 1988). Therefore, in the 1960s, the possible relationship between the piggery density and the incidence of JE was evaluated in 13 prefectures (Kumamoto, Saga, Fukuoka, Tokushima, Kagawa, Yamaguchi, Tottori, Okayama, Hyogo, Kyoto, Shiga, Mie, and Osaka) where 20.0% or more (23.1-68.0%) municipalities showed 15.0% or more paddy fields.

As Table 1 shows, the correlation coefficient (r) was only 0.52. The relationship observed in the 1970s, i.e., increases in the incidence relative to increases in the piggery density, was not observed in the 1960s.

<table>
<thead>
<tr>
<th>Years</th>
<th>No. of prefectures</th>
<th>Correlation coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>1960s</td>
<td>13</td>
<td>0.52</td>
</tr>
<tr>
<td>1970s²</td>
<td>9</td>
<td>0.83*</td>
</tr>
</tbody>
</table>

**p<0.01.

¹: Mean no. of swine farms per krf in districts.
²: Data from Nakamura (1988).
Relationship between the cowshed / piggery density ratio and the JE epidemics

Prefectures were classified into those showing a higher density of cowsheds than piggeries and those showing a higher density of piggeries than cowsheds, and the possible relationship between the piggery density and the incidence of JE was evaluated. In each prefecture, the ratio of the sum density of cowsheds and stables to the piggery density (CH/S ratio) and the ratio of cowsheds density to the sum density of piggeries and stables (C/HS ratio) in 1960, 1970, and 1980 were calculated. The mean of the values in 1960 and 1970 was defined as the value of the 1960s, and the mean of the values in 1970 and 1980 as the value of the 1970s.

Cx. tritaeniorhynchus preferably feeds on horses (Sasa et al., 1950). The turnover of generations is slower in horses than in swine. However, an experimental study showed that horses develop viremia after JE virus infection and infect Cx. tritaeniorhynchus (Gould et al., 1964). The number of horse-breeding farms had markedly decreased by the 1970s. In the 1960s, the state of horse breeding markedly differed among prefectures. There were only 56–958 horse-breeding farms in Kagawa, Kyoto, Shiga, Mie, Wakayama, and Osaka Prefectures, but 12,000–33,000 farms in Kagoshima, Miyazaki, Kumamoto, Oita, and Fukuoka. However, these figures were lower than the number of beef cattle-breeding farms (27,000–118,000).

The distribution of the CH/S ratio (figure not shown) showed no prefectures with a CH/S ratio of 10.6–12.9 in the 1960s or a CH/S ratio of 8.0–13.1 in the 1970s. Therefore, analysis was performed after the 22 prefectures were divided into those showing a CH/S ratio ≥ 13.0 and those showing a CH/S ratio < 13.0. Since there were also no prefectures showing a C/HS ratio of 10.6–12.9 (figure not shown), evaluation was done after the 22 prefectures were similarly divided.

As described above, no relationship was observed between the piggery density and the incidence of JE in the 1960s even in the 13 prefectures where 20.0% or more of the municipalities showed a paddy field ratio of more than 15.0%. Therefore, analysis was done after these 13 prefectures were classified into those with a CH/S ratio ≥ 13.0 and those with a CH/S ratio < 13.0.

As Table 2 shows, no association was observed between the piggery density and the incidence of JE (r = -0.08) in prefectures showing a CH/S ratio ≥ 13.0. In prefectures showing a

<table>
<thead>
<tr>
<th>CH/S</th>
<th>No. of prefectures</th>
<th>Correlation coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>over 13.0</td>
<td>6</td>
<td>-0.08</td>
</tr>
<tr>
<td>under 12.9</td>
<td>7</td>
<td>0.87*</td>
</tr>
</tbody>
</table>

*p<0.05.

1: Mean no. of swine farms per km2 in districts.

2: Ratio of the sum of the mean densities of cowsheds and stables to the mean piggery density.

Table 2. Correlation coefficients between the average incidence of JE cases and the mean piggery density1 at two different CH/S ratios2, in prefectures where the percentage of districts with a paddy field ratio of more than 15.0% was over 20.0%, among 22 prefectures in southwest Japan during the 1960s.
CH/S ratio $< 13.0$, the incidence increased with the piggery density ($r = 0.87$).

In the 1960s, cattle did not play a role in the JE epidemics.

Fig. 1 shows the association between the piggery density and CH/S ratio in the 1960s and 1970s in prefectures where 20.0% or more municipalities showed a paddy field ratio of 15.0% or more compared to other prefectures.

The CH/S ratio increased as the piggery density approached zero but sharply decreased as the piggery density approached 1.0. Though marked variation was observed in the inflection range, the CH/S ratio as a whole showed a curve. Therefore, when the 22 prefectures were classified, whether the piggery density was 1.0 or more was also taken into consideration, and the relationship between the piggery density and the incidence of JE was analyzed. The CH/S ratio was generally lower in the 1970s than in the 1960s. Even in the 1970s, there were some prefectures showing a low percentage of municipalities with a paddy field ratio of 15.0% or more, a locally very high piggery density, or a CH/S ratio similar to that in the 1960s. However, the piggery density was $< 1.0$, and the CH/S ratio was $\leq 10.0$ in 9 prefectures that showed a low
piggery density and a low CH/S ratio in the 1970s. In the 1960s, there were prefectures showing a low piggery density but a very high CH/S ratio.

Therefore, analysis was performed after classification of the 22 prefectures into those showing a CH/S ratio $\geq 13.0$ and a piggery density $< 1.0$ (a high CH/S ratio and a low piggery density) compared to other prefectures.

The flight range of *Cx. tritaeniorhynchus* is larger, at least 1km as the ordinary activity range (Wada et al., 1969). Therefore, when the piggery density was $\geq 1.0$, piggeries were present anywhere in the ordinary activity range of this mosquito species. When the piggery density was $< 1.0$, there were some districts in which piggeries are absent, and only cowsheds were present. Not only the CH/S ratio but also such differences in piggery density may affect the incidence of JE virus infection in humans.

The 22 prefectures were classified into two groups showing a high CH/S ratio and a low piggery density or the other findings. In each group, the relationship between the piggery density and the incidence of JE was evaluated in prefectures where municipalities showing a paddy field ratio of 15.0% or more accounted for $\geq 0\%$, $\geq 10.0\%$, $\geq 20.0\%$.

Table 3. Correlation coefficients between the average incidence of JE cases and the mean piggery density$^1$ at two different CH/S ratios$^2$ and the mean piggery density, by a percentage of districts with a paddy field ratio of more than 15.0% in 22 prefectures in southwest Japan during the 1960s.

<table>
<thead>
<tr>
<th>CH/S ratio (Piggery density)</th>
<th>% of districts with a paddy field ratio of more than 15.0% in each prefecture</th>
<th>No. of prefectures</th>
<th>Correlation coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>over 13.0</td>
<td>more than 15.0%</td>
<td>8</td>
<td>0.83**</td>
</tr>
<tr>
<td>(less than 13.0)</td>
<td>10.0</td>
<td>7</td>
<td>0.84*</td>
</tr>
<tr>
<td>0.9</td>
<td>20.0</td>
<td>5</td>
<td>0.95*</td>
</tr>
<tr>
<td>all cases</td>
<td>more than 15.0%</td>
<td>14</td>
<td>0.43</td>
</tr>
<tr>
<td>except</td>
<td>15.0%</td>
<td>10</td>
<td>0.88**</td>
</tr>
<tr>
<td>the above</td>
<td>20.0%</td>
<td>8</td>
<td>0.88**</td>
</tr>
</tbody>
</table>

$^1$p<0.05, **p<0.01.

$^1$: Mean no. of swine farms per km$^2$ in district.

$^2$: Ratio of the sum of the mean densities of cowsheds and stables to the mean piggery density.

As Table 3 shows, in the prefecture group showing a high CH/S ratio and a low piggery density, the incidence of JE increased with a piggery density regardless of the percentage of municipalities with a paddy field ratio of 15.0% or more. In the other prefecture group, no association was observed between the piggery density and the incidence of JE in prefectures where municipalities showing a paddy field ratio of 15.0% of more accounted for $\geq 0\%$, but a relationship was observed in the prefectures where such municipalities accounted for $\geq 10.0\%$.

Thus, evaluation after classification of the prefectures according to the CH/S ratio and piggery density also revealed a relationship between piggery density and the incidence of JE in the 1960s. Therefore, in the 1970s, when the paddy field area was decreased compared with
Table 4. Correlation coefficients between the average incidence of JE cases and the mean piggery density\(^1\) at two different CH/S ratios\(^2\) and the mean piggery density, by a percentage of districts with a paddy field ratio of more than 15.0% in 22 prefectures in southwest Japan during the 1970s.

<table>
<thead>
<tr>
<th>CH/S ratio (Piggery density)</th>
<th>% of districts with a paddy field ratio of more than 15.0% in each prefecture</th>
<th>No. of prefectures</th>
<th>Correlation coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>over 13.0 (less than 0.9)</td>
<td>more than 0 %</td>
<td>4</td>
<td>—</td>
</tr>
<tr>
<td>all cases</td>
<td>more than 0 %</td>
<td>18</td>
<td>0.07</td>
</tr>
<tr>
<td>except</td>
<td>10.0</td>
<td>14</td>
<td>0.24</td>
</tr>
<tr>
<td>the above</td>
<td>20.0</td>
<td>8</td>
<td>0.77(^*)</td>
</tr>
</tbody>
</table>

\(^p<0.05.\)
\(^1\): Mean no. of swine farms per \(\text{ha}\) per district.
\(^2\): Ratio of the sum of the mean densities of cowsheds and stables to the mean piggery density.

the 1960s, evaluation was performed according to the CH/S ratio and piggery density. As shown in Table 4, only 4 prefectures showed a high CH/S ratio and low piggery density. In addition, only in Hyogo Prefecture, municipalities with a paddy field ratio of 15.0% or more accounted for \(\geq 20.0\%\). Therefore, these 4 prefectures were excluded from analysis.

The other 18 prefectures were classified into prefectures where municipalities showing a paddy field ratio of 15.0% or more accounted for \(\geq 0\%\), \(\geq 10.0\%\), or \(\geq 20.0\%\), and the coefficient of the correlation between the piggery density and the incidence of JE was calculated. A correlation was observed in only 8 prefectures where municipalities showing a paddy field ratio of 15.0% or more accounted for \(\geq 20.0\%\). This finding was similar to that observed when the prefectures were not classified according to the CH/S ratio and piggery density (Nakamura, 1988). However, the correlation coefficient was not very high, despite the classification according to the CH/S ratio and piggery density. As previously reported (Nakamura, 1988), this may be due to inclusion of prefectures such as Kagawa Prefecture where the incidence was very low though the percentage of municipalities with a paddy field ratio of 15.0% or more and the piggery density were quite high\(^1\).

Thus, a correlation between the piggery density and the incidence of JE was observed in prefectures showing a high CH/S ratio and a low piggery density even when paddy fields were not much developed. In other prefectures, a correlation between the piggery density and the incidence of JE was observed only when paddy fields were adequately developed.

Similarly, the relationship between the sum of the piggery and stable densities and the incidence of JE was calculated. As shown in Table 5, only 5 prefectures showed a C/HS ratio \(\geq 13.0\) during the 1970s, complete drainage of paddy fields from late July to early August had become common practice in water management throughout the prefecture (Miyashita, 1992). This may be partly the cause of the lower population of Cx. tritaeniorhynchus and decrease in JE epidemics.
Table 5. Correlation coefficients between the average incidence of JE cases and the sum of the mean density\(^1\) of piggeries and stables at two different C/HS ratios\(^2\) and the sum of the mean densities of piggeries and stables, by a percentage of districts with a paddy field ratio of more than 15.0% in 22 prefectures in southwest Japan during the 1960s.

<table>
<thead>
<tr>
<th>C/HS ratio (Total density of piggeries and stables)</th>
<th>% of districts with a paddy field ratio of more than 15.0% in each prefecture</th>
<th>No. of prefectures</th>
<th>Correlation coefficient</th>
</tr>
</thead>
<tbody>
<tr>
<td>over 13.0 (less than 0.9)</td>
<td>more than 10.0%</td>
<td>5</td>
<td>0.50</td>
</tr>
<tr>
<td>all cases</td>
<td>more than</td>
<td>17</td>
<td>0.23</td>
</tr>
<tr>
<td>except</td>
<td>10.0</td>
<td>12</td>
<td>0.36</td>
</tr>
<tr>
<td>the above</td>
<td>20.0</td>
<td>9</td>
<td>0.45</td>
</tr>
</tbody>
</table>

\(^1\): The sum of mean no. of swine farms and stables per kilometer per district.

\(^2\): Ratio of the mean density of cowsheds to the sum of the mean densities of piggeries and stables.

and a sum of the piggery and stable densities < 1.0. The relationship between the sum density and the incidence of JE was evaluated only in prefectures where municipalities showing 15.0% or more paddy fields accounted for ≥ 10.0%. However, the correlation coefficient was low. Other prefectures were subclassified into those where municipalities showing a paddy field ratio of 15.0% or more accounted for ≥ 0%, ≥ 10.0%, or ≥ 20.0%, and the correlation coefficient was calculated. However, no association was observed between the sum density and incidence.

The relationship between the piggery density and the JE incidence shown in Table 3 was compared between the 1960s and 1970s only in prefectures where municipalities with a paddy field ratio of 15.0% or more accounted for ≥ 20.0% (Fig. 2).

As shown in this figure, though a correlation was observed between the piggery density and the incidence of JE, the degree of increase in the incidence relative to the piggery density markedly differed by the period or the CH/S ratio. The regression coefficient obtained from the linear relationship between the piggery density and the incidence of JE was highest (b = 5.53) at a high CH/S ratio and a low piggery density and was low (b = 0.46) under other conditions in the 1960s. However, the latter value was higher than that in the 1970s (b = 0.14).

In the 1960s, not only the population of *Cx. tritaeniorhynchus* but also the number of infected mosquitoes may have been lower in prefectures with a high CH/S ratio and a low piggery density compared to those in other prefectures. Nevertheless, in the prefectures with a high CH/S ratio and a low piggery density, a high incidence similar to that in other prefectures was observed at a piggery density approximately 1/10 of that in the other prefectures. At the same piggery density, the incidence in the 1970s was lower than that in the 1960s. This may be partly due to a decrease in the density of feeding sources other than swine in the paddy field area.
Fig. 2. Relation of the incidence of JE cases to the mean piggery density\(^1\) at two different CH/S ratios\(^2\) and the mean piggery density, in prefectures where the percentage of districts with a paddy field ratio of more than 15.0% was over 20.0%, among 22 prefectures of southwest Japan during the 1960s (white) and 1970s (black). See also Table 3 and 4.

\(^1\): Mean no. of swine farms per km\(^2\) in districts. \(^2\): Ratio of the sum of the mean densities of cowsheds and stables to the mean piggery density. \(r\): correlation coefficients. \(b\): regression coefficient. Triangles: CH/S ratio was over 13.0 and the mean piggery density was less than 0.9. Circles: All cases except triangles. The arabic numerals in diagram show the prefectures as follows: 1: Kumamoto, 2: Saga, 3: Fukuoka, 4: Tokushima, 5: Kagawa, 6: Yamaguchi, 7: Tottori, 8: Okayama, 9: Hyogo, 10: Kyoto, 11: Shiga, 12: Mie, 13: Osaka.

**DISCUSSION**

Only in districts with a large population of mosquitoes, the timing of the peak vector infection rate, i. e., whether it was earlier or later than the peak in the rise and decline in the seasonal prevalence of mosquitoes, has a significant impact on the transmission of the virus from the mosquito-swine cycle to humans (Yamamoto, 1981, 1984; Nakamura et al., 1992b). In districts with appropriate environmental conditions for the breeding of *Cx. tritaeniorhynchus*, a transmission cycle of JE virus is often established at an early stage in the epidemic period, and a large number of infected mosquitoes are generated (Nakamura et al., 1992b). The incidence of JE was
high in the prefectures showing a high CH/S ratio and a low piggery density though the piggery density in these prefectures was approximately 1/10 of that in the other prefectures, thus, a build-up of dense population of infected mosquitoes was not considered. The following conditions are required to achieve this high incidence; i ) dispersion of infected mosquitoes from districts where a JE virus transmission cycle is established at an early stage in the epidemic period under appropriate environmental conditions to other districts, and ii ) a difference in the opportunity for human infection between prefectures with a high CH/S ratio and a low piggery density and the other prefectures. Concerning i ), JE virus transmission cycle should be established in the entire prefecture over a short period earlier than the peak in seasonal prevalence of Cx. tritaeniorhynchus. Indeed, in Osaka Prefecture, which once showed a high CH/S ratio and a low piggery density, the interval between the first appearance of 2ME sensitive antibody and the observation of an HI antibody positive rate of 100.0% in swine at the slaughterhouses was shorter in years when the number of patients ranged between 71 - 346 than in years when there was no patients, and the interval in years when the number of patients was 1 - 20 was between these two values (Kimura et al., unpublished data).

Cx. tritaeniorhynchus prefers cattle to swine and much prefers swine to humans (Barnett, 1960; Pennington and Phelps, 1966; Wada et al., 1970; Mitchell et al., 1973; Reuben et al., 1992). Since cattle are more nervous than swine in response to mosquito feeding, feeding becomes increasingly difficult at a lower mosquito density in cattle than in swine (Fujito et al., 1971). The flight range of Cx. tritaeniorhynchus is considerable. Since its general activity range includes at least 1km (Wada et al., 1969), the CH/S ratio, which indicates the density ratio per km², represents the value in an area where mosquitoes actually select hosts. Therefore, we speculate the following.

A transmission cycle is established at an early stage in the epidemic period in piggeries under appropriate environmental conditions. An increase in the population of mosquitoes in these piggeries makes feeding of infected mosquitoes difficult. The mosquitoes disperse seeking other feeding sources, and a transmission cycle becomes established in other piggeries. At this stage, the abundance of mosquitoes in districts under less-appropriate environmental conditions may reach the level at which feeding on cattle is difficult. The dispersed infected mosquitoes have more opportunity to find cowsheds in prefectures with a high CH/S ratio and a low piggery density but piggeries in other prefectures. Feeding is difficult in cowsheds but not yet in piggeries. Therefore, in prefectures with a high CH/S ratio and a low piggery density, infected mosquitoes continue to disperse until they find piggeries. In other prefectures, dispersion does not occur until a further increase in the mosquito population makes feeding difficult. As a result, cattle promote the dispersion of mosquitoes because of their intolerance to mosquito feeding while swine delay the dispersion due to their indifference. Of course, these differences due to the CH/S ratio change with environmental conditions, i.e., the ratio of districts under appropriate environmental conditions to the entire prefecture, in both the prefectures with a high CH/S ratio and a low piggery density and the other prefectures, especially the latter. That is, in the prefecture with the very high ratio of districts under appropriate environmental conditions, a transmission cycle is established almost synchronously in the far greater number of piggeries throughout the
prefecture. Therefore, delayed mosquito dispersion played by swine no longer have the role in epidemics of JE.

From the perspective ii), the opportunity for human infection may locally increase at a mosquito population level that makes feeding on cattle difficult in prefectures with a high CH/S ratio and a low piggery density including districts with cowsheds only and not piggeries.

The opportunity for dispersed infected mosquitoes to find other piggeries, i.e., the opportunity for humans to escape feeding, increases at a lower CH/S ratio and higher piggery density. Together with delayed mosquito dispersion, this may be a cause of the differences in the regression coefficient according to the CH/S ratio in Fig. 2. Since the dispersion of mosquitoes occurs at each piggery as a unit, large scale breeding farms have a larger number of swine per piggery, and have recently been increasing, this may have preventive effects on the dispersion of mosquitoes, decreasing the opportunity for human infection. A study using a mathematical model reported a decrease in the risk for human infection with an increase in the number of swine (Mogi and Sota, 1991; Sota, 1992).

However, for the establishment of such an epidemic process, dispersion depending on the density of mosquitoes including infected ones should occur in each cowshed or piggery as a unit.

In Cx. tarsalis and Cx. tritaeniorhynchus, as the mosquito density increases, the feeding rate decreases, and percentage of mosquitoes that can suck only a little blood increases (Dow et al., 1957; Fujito et al., 1971). An experimental study in Aedes aegypti showed that partially engorged mosquitoes continuously seek hosts (Klowden and Lea, 1978). Indeed, partially engorged Cx. tarsalis, were collected in the field (Mitchell and Millian, 1981). A unimodal host-seeking rhythm with maximal activity generally occurs 1-4 hours after sunset. However, this peak disappears with an increase in the mosquito population, resulting in continued host-seeking activity throughout the night. This was suggested to be due to host-avoidance reactions stimulated by elevated mosquito attack rates in birds, making mosquito feeding difficult (Reisen and Reeves, 1990).

No such findings have been clarified in Cx. tritaeniorhynchus. Though cattle become nervous in response to mosquito feeding, their anti-mosquito behaviour may not be as effective as that in birds, the most attractive host to Cx. tarsalis. Sasa et al., (1950) reported that Anopheles sinensis is greedy and continues to feed even when animals move slightly while Cx. tritaeniorhynchus is very cowardly during feeding and feeds relatively well on resting sheep at night but rarely on moving sheep. In addition, the percentage of partially engorged Cx. tritaeniorhynchus increases, depending on the mosquito density (Fujito et al., 1971). In certain district, JE patients were observed not in the year when the estimated number of infected mosquitoes in July-August (sum of the number of collected mosquitoes in the week when the JE virus was isolated X the isolation rate) was highest but in the year when the estimated number of infected mosquitoes from the first week when JE virus was isolated to the week when the number of collected mosquitoes reached a peak, was highest, though the absolute value in the latter was only 1/3 of that in the former (Nakamura et al., 1987). These findings suggest density-dependent dispersion of Cx. tritaeniorhynchus.

Thus, the JE epidemics in the 1960s were characterized by the major role played by cattle
in some prefectures showing a high CH/S ratio and a low piggery density. In other prefectures, swine did not cause effective dispersion of infected mosquitoes. In such prefectures, since a large number of mosquitoes must be recruited for their dispersion, an adequate paddy field area and a high piggery density may be needed to promote a large epidemic. These conditions were fulfilled in the 1960s. Of course, in prefectures other than those with a high CH/S ratio and a low piggery density, the presence of cowsheds may also have influenced the abundance of *Cx. tritaeniorhynchus*. However, the barn density per unit area was limited, and therefore, the role of cattle in the occurrence of the epidemic may have been less in prefectures showing a higher piggery density and a larger epidemic.

Sometimes, many patients are observed even under such an unfavorable environmental conditions as in Osaka city where piggeries do not often coexist with paddy fields (Nakamura et al., 1992a). Infected mosquitoes after egg laying may have fewer opportunities to find piggeries again, increasing the opportunity for feeding on humans.

In this study, the density of cowsheds and that of stables were evaluated as a whole. Therefore, the host preference of *Cx. tritaeniorhynchus* among cattle, swine, and horses is unclear. The degree of anti-mosquito behaviour in horses is also unclear. Though it is unlikely that horses are as indifferent as swine to mosquito feeding, the role played by horses in JE epidemics in the 1960s has remained unsettled.

The recent low epidemics of JE has been suggested to be partly due to the spread of vaccination in children aged 3–15 years (Oya, 1979). The degree of human immunization is an important factor affecting the size of epidemics. However, the degree of human immunization in the 1960s was unclear in the 22 prefectures analyzed in this study. In the 1970s, the incidence of JE was also high in Kyushu. However, since the degree of immunization was similar between Kyushu and other areas showing a low incidence of JE, the high incidence in Kyushu can not be explained by the degree of human immunization (Oya, 1979). Therefore, in the 1960s also, it is difficult to explain the marked differences in the incidence of JE among the 22 prefectures by the degree of human immunization alone. The differences in environmental conditions analyzed in this study should be also taken into consideraration.

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148


