Breeding Ecology of *Motacilla alba* and *M. grandis* and their Interspecific Relationship

Syuya Nakamura*, Hiroyuki Hashimoto** and Osamu Sootome***

**Abstract** The breeding season of the White wagtail *Motacilla alba* (from April to July) completely overlapped that of the coexisting Japanese wagtail *Motacilla grandis* which bred in and around towns. Both species built their nests on buildings, and some of these two species used exactly the same nest sites. Males of the White wagtail contributed to 8% of nest building, 6% of incubation, 36% of chick-feeding and 28% of faecal sac removal. These contributions were less than those of the male Japanese wagtail in incubation and chick-feeding. One of the two main food items for nestlings of both species was found to be the same, that is, the insect family Tipulidae.

Japanese wagtails obviously dominated White wagtails in the breeding season. Although the interspecific aggressiveness of Japanese wagtails towards White wagtails was not so severe as that towards conspecifics, it was sufficient to decrease the male White wagtail’s part in incubation. This aggressiveness may be a cause of habitat segregation between the two species in the overlapping part of their breeding ranges.

**Introduction**

Recently the White wagtail, *Motacilla alba lugence*, has expanded its breeding range southward along the Coast of the Japan Sea (Nakamura 1978). As its breeding range has also extended to the inland of the Honshu Island, the interspecific relationship between the White wagtail and the Japanese wagtail, *Motacilla grandis*, a closely related species, has become an objective of studies. The breeding habitats of the White wagtails are streams without gravelly shores, factory areas with narrow water ways and town areas, while the Japanese wagtails inhabit around rivers with gravelly shores in high density (Higuchi & Hirano 1981). The breeding biology, social behaviour and territory of the Japanese wagtail have already been studied (Haneda & Shinoda 1969, Hirano 1981 and Nakamura 1982). While most studies of the White wagtail have been on wintering behaviours (Davies 1976, Watanabe & Maruyama 1977 and Zahavi 1971); the breeding aspects remain to be elucidated. And the interspecific relationships between the two species have not yet been described. It is of great interest to see whether the extension of breeding range of the White wagtail has been proceeding under the influence of the Japanese wagtail, or whether it has nothing to do with it. Whether it has been affecting the breeding distribution of the Japanese wagtail or not is also interesting to observe.

The purpose of this paper is firstly the clarification of the breeding biology of the White wagtail and to compare it with that of the Japanese wagtail. Secondly the in-
interspecific relationship is referred to under the observation of the behavioural interference between the two species, which overlapped in their home ranges.

Methods

The field surveys were carried out on the campus of the Ibaraki University and in the northerly situated rice fields in the northern part of Mito City, Ibaraki Prefecture (Fig. 1). The campus and the rice fields are situated on the upper and the lower flats of
a long fluvial terrace of the Naka River, respectively. The intervening slope is occupied by the dense wood. Most of the periphery of the campus on the upper flat are residential areas, except for small crop fields at the north side of the campus. On the lower flat narrow irrigation and drainage ditches, 1-2 meters in width, run through the rice fields. Details of this study area and the distribution of the Japanese wagtail were shown in the preceding paper (1982). Only one pair of the White wagtail bred in the study area.

The study periods were from 1978 to 1980 over three breeding seasons. The position of each individual was traced on maps (1/2500). Every behaviour was observed and the time when it occurred was recorded, as precisely as possible. Each Japanese wagtail in the study area was discriminated by colour banding. So were the White wagtails in 1978, but ones in 1979 and 1980 were discriminated by body colour patterns.

Observation on the nests was made from sunrise to sunset. Eggs and nestlings were measured with slide callipers and weighed to the nearest 10 mg with balances.

Results

I. Breeding

1. Breeding stages

Fig. 2 shows the breeding stages of the White wagtail and the Japanese wagtail in the study area. Breeding stages of the White wagtail are as follows; the nesting stage (about 16 days for the first brood, 5 days for the second brood and repeat broods), the egg-laying stage (4 to 5 days), the incubating stage (about 14 days), and the fledgling stage (unknown). The durations of each stage is similar to that of the Japanese wagtail (Haneda & Shinoda 1969, Nakamura 1982).

The earliest start of the first egg-laying of the White wagtail was on April 27, 1978. This was much later than the earliest first egg-laying day (March 16, 1979) as well as the averaged first egg-laying day (March 31) of the Japanese wagtail (Nakamura 1982). This lateness of the initiation of breeding season in the White wagtail was also suggested by Higuchi & Hirano (1981). The breeding season of the White wagtail around the study area seems to be from April to July, taking data of other areas of Mito City into consideration. This period is well overlapped by the breeding season of the Japanese wagtail.

Haneda & Shinoda (1969) denied the second brood in the Japanese wagtail, however in this study area the second brood was commonly observed and the third ones was also attempted. While in the White wagtail, the second brood might be rare even if we referred other examples of its breeding in Mito City.

2. Nest Building

All the observed nests of the White wagtail, four in the study area and eight in the other part of Mito City, were built in buildings. Thirteen of fifteen breeding nests of the Japanese wagtail were built on the ground (Haneda & Shinoda 1969). But around this study area 24 of 30 nests were built in clefts or under all kinds of shelters on a roof of buildings. Some of the nest sites were shared by both species but at different times.
Breeding stages of Japanese wagtail showed only for those pairs whose home ranges overlapped with those of a pair of White wagtail.

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Fig. 2. Breeding stages.

Breeding stages of Japanese wagtail showed only for those pairs whose home ranges overlapped with those of a pair of White wagtail.

Fig. 3. Daily change of carrying nesting materials in White wagtail, on April 19, 8th day of nesting stage.

Females and males of both species scouted round for sites suitable for nests before nest buildings. In the White wagtail the nest was accomplished at the site where a male first brought nesting material and a female then followed him closely behind. In the Japanese wagtail the nest was completed at the site where a female followed a male closely and where singing took place. About an hour later, the female then began to
bring in nesting material. Whether the final decision was made by a male or a female
was unknown, however, there was surely the close exchange of behaviours between a
male and a female of the pair in deciding a nest site in both species.

Frequency of carrying materials per day in the first nesting of the White wagtail in
1978 was less than 10 times in total for both male and female during the first six days
(April 12 to 17). It increased to 61 times on April 19, and then the cup of the nest was
completed. The peak of carrying materials during a day was at about 0900 o’clock,
and the birds carried far less nesting materials in the afternoon (Fig. 3). A male shared
8% of nest building with a female. It took ten days to complete the first nest using
the old nest. But, the nests of repeated brood was also built afresh and completed in
five days. The pair didn’t bring nesting material on rainy days for the first nest but did
in the repeated nest. Shortening of the nesttng stage as such was also observed in the
repeated brood or after the second brood in the Japanese wagtail (Nakamura 1982) and in
the third brood of the skylark, *Alauda arvensis* (Haneda & Obuchi 1967).

3. Egg-laying and Incubation

The female of the White wagtail laid an egg each day early in the morning at about
0400 o’clock until she completed the clutch (Table 1). As the number of eggs increased,
laying time became earlier and staying time in the nest for egg-laying longer. The
female quivered her wing and moved her body up and down slightly just before laying
the egg.

Although incubation of the White wagtail was done even just after laying eggs and
in the daytime in egg-laying stage, full incubation started after the day when a clutch was
completed or the day before. Incubation in the daytime was done by both a male and
a female, while at night it was done only by the female.

The female left her nest at frequent intervals in the daytime (on an average, 8.2 min-
utes off followed by 22.1 minutes on the nest). When the female left of her own accord,
she spent on the average of 6.7 minutes off and 20.7 minutes on. When she left on ac-
count of her mate’s visit or when he called near the nest, however, she did 15.9 minutes
off and 29.5 minutes on. Then the period of the female off the eggs increased more
than twofold and her unit incubation time became longer about 40 percent.

Daily changes of incubation time in the first and the repeated brood of the White
wagtail are shown in Fig. 4. The incubation by the male was rare in the morning and
the evening, however showed a peak around midday (Fig. 5). More than seventy per-
cent of male’s incubation took place from 1100 to 1300 o’clock. Unit incubation time
of the male was short and irregular as compared to that of female. Such a tendency was

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<td>'78 May 24</td>
<td>First</td>
<td>4: 17–4: 34 (17)</td>
<td>4: 32</td>
</tr>
<tr>
<td>May 25</td>
<td>Second</td>
<td>4: 08–4: 41 (33)</td>
<td>4: 30</td>
</tr>
<tr>
<td>May 26</td>
<td>Third</td>
<td>4: 12–4: 50 (38)</td>
<td>4: 23</td>
</tr>
<tr>
<td>May 27</td>
<td>Fourth</td>
<td>4: 09–4: 52 (43)</td>
<td>4: 18</td>
</tr>
</tbody>
</table>
Fig. 4. Daily change of incubating time in White wagtail.

a. first brood, the last fifth egg laid on April 27.
b. repeated brood, the last fifth egg laid on May 28.

observed in the Japanese wagtail (Fig. 6 and Haneda & Shinoda 1969). Night incubation was also done in only by the female in the Japanese wagtail.

The total incubation time per day by both male and female of the White wagtail didn’t vary markedly through the incubating stage in the first brood: 1275 minutes (third days after full incubation started), 1168 (fifth), 1172 (eighth), 1175 (tenth) and 1308
There was a tendency for male's total incubation time per day to increase; 12 minutes (3rd), 24 (5th), 16 (8th), 44 (10th) and 119 (12th). This tendency was contrary to that of the Japanese wagtail (Haneda & Shinoda 1969). In the repeated brood, the male hardly incubated and the total incubation time was less than that of the first brood. This will be discussed later in relation to the interference by the Japanese wagtail. Share of daytime incubation of the White wagtail in the first brood was 6% in male, which is much less than that of the male Japanese wagtail, 27.9% (Haneda & Shinoda 1969).

Three types of incubation changeover (Wallraff 1953) were all observed in the White wagtail. Type I and Type II were frequently observed in females; the former is the changeover by an approach or a call of the relief, and the latter is the case of the relief entering the nest and taking turn on it. On the other hand, Type III was seen almost exclusively in males; they spontaneously left the nest without waiting for alternation. This shows that the female is more eager to incubate than the male. Haneda & Shinoda
Fig. 6. Daily change of relative incubation time in Japanese wagtail, showing daytime incubation time per hour in percentage.

(1969) showed that Type II wasn’t observed in the Japanese wagtail. In this study, however, three types of changeover were all observed in the Japanese wagtail as well as in the White wagtail. This may be related to the characters of individual birds or the circumstances around the nesting site.

The parents of the White wagtail turned their eggs during incubation. Turning eggs was observed 3.4 times per hour on the average and 10 times per hour at maximum. The female sometimes covered her eggs with nesting material, pulled out from the lining of the nest, when she left the nest.

4. Brooding

In the first half of the nestling stage a female of the White wagtail brooded her chicks right after feeding in the daytime, but a male didn’t do so. The female brooded through the night. Total brooding time in the daytime decreased as nestlings grew up; 339 minutes (22.6 minutes per hour) in the third day (June 10) after hatching and 28 minutes (4.6 minutes per hour) in the sixth day (June 13). After the sixth day the female didn’t brood them at night.

Brooding in the Japanese wagtail was done by the female but not by the male (Hanedea & Shinoda 1969). In this study, however, a male brooded a little. Total brooding time in the daytime was 261 minutes (20.1 minutes per hour) in the female and 20 minutes in the male in the third day after hatching. The female only participated in night brood-
Fig. 7. Daily change of brooding time (the third day of nestling stage, June 10 in White wagtail, April 11 in Japanese wagtail).

Daytime brooding of both species was observed most frequently in the morning and in the evening that continued to night brooding, and less frequent in the midday (Fig. 7).

5. Feeding

Food of nestlings for the White wagtail was exclusively of animal matters (insects 85.4%, and spiders 14.6%, by numbers), in which Diptera was composed of the greater parts (56.1%), especially crane flies (Tipulidae) (Table 2). In most cases parents fed their nestlings with the whole animal. But, they gave a gadfly deprived of its wings to their nestlings.

Table 2. Foods for nestlings.

<table>
<thead>
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<th></th>
<th>White wagtail</th>
<th>Japanese wagtail</th>
<th>(% fresh weight)</th>
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<tr>
<td>Diptera</td>
<td>*Tipulidae</td>
<td>*Tipulidae</td>
<td>20.5</td>
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<td>Psychodidae</td>
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<td>Scarabaeidae</td>
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<tr>
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<td>—</td>
<td>Geometridae</td>
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<td></td>
<td>—</td>
<td>Amatidae</td>
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</tr>
<tr>
<td>Neuroptera</td>
<td>Chrysopidae</td>
<td>—</td>
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</tr>
<tr>
<td>Odonata</td>
<td>Agrionidae</td>
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<tr>
<td></td>
<td>Libellulidae</td>
<td>—</td>
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<tr>
<td>Hemiptera</td>
<td>Gerridae</td>
<td>—</td>
<td></td>
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<tr>
<td>Orthoptera</td>
<td>—</td>
<td>Gryllotalpidae</td>
<td>59.3</td>
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<td></td>
<td>—</td>
<td>Tettigidae</td>
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<tr>
<td>Aranea</td>
<td>*Atridae</td>
<td>*Lycosidae</td>
<td>7.9</td>
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<tr>
<td></td>
<td>—</td>
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Sample size 41 123

* Two families of most numerous foods in each species.
Table 3. Frequency of feeding types in White wagtail.

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<th>Total</th>
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<td>6</td>
<td>10</td>
</tr>
<tr>
<td>II</td>
<td>44</td>
<td>54</td>
<td>56</td>
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<tr>
<td>III</td>
<td>15</td>
<td>4</td>
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<tr>
<td></td>
<td>Total</td>
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<td>155</td>
</tr>
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F: Female, M: Male, N: Nestling

Fig. 8. Daily change of relative feeding rate. Showing feeding rate per hour in percentage, averaged each observation day.  

a: White wagtail,  
b: Japanese wagtail.
The feeding pattern of the White wagtail was divided into three types; Type I: the female feeds nestlings, Type II: the male feeds nestlings, and Type III: the males delivers foods to the female who feeds nestlings. In case that food brought in is much in quantity, the male delivers a part of food to the female and feeds the rest to nestlings. Type III was observed when females brooded (Table 3). The daily fluctuation of feeding rate in females was relatively constant (Fig. 8-a). In males the amplitude of fluctuation of feeding rate was larger than in females. A feeding rate per day per nestling increased as the nestling stage proceeded (Fig. 9). In the White wagtail a male and a female shared 36% and 64% of feeding, respectively. Male’s share was less than that of the Japanese wagtail, that is, 53.8% (Haneda & Shinoda 1969).

Foods of nestlings of the Japanese wagtail obtained by collar method was composed of insects (87.8% by numbers, 92.1% by fresh weight) and spiders (see Table 2). The most numerous food was adult crane flies, *Tipula* (74.0% by numbers, 16.2% by fresh weight), and the heaviest one was the adult of mole crickets, *Gryllotalpa africana* (58.9% by fresh weight, 4.9% by numbers). One individual of the mole cricket was observed to be brought in each visit and most of their heads were removed from the bodies. Feeding types observed in the Japanese wagtail were Type I and II. The amplitude of fluctuation of feeding rate in males was higher in females (Fig. 8-b). A feeding rate per day per nestling before fledging increased about twoce as compared with that obtained right after hatching (Fig. 9).

Food items shown in Table 2 were obtained from the nests of the White wagtail and
the Japanese wagtail which bred at a distance of 230 meters apart, having an interval of about one month. Crane flies which were the important food of both species emerged abundantly in the ditches of rice fields in the spring. The pair of the Japanese wagtail gathered mole crickets at tilling rice fields. The pair of the White wagtail showed a tendency to gather foods more frequently on the campus than the Japanese wagtail. According to Haneda & Shinoda (1969), Japanese wagtails plentifully fed on Ephemeroptera and Plecoptera, however in this study they brought them in very little. This may be due to the differences of habitats in each study area; the study of Haneda & Shinoda (1969) was carried out along a large river. Both species were insectivores and they fed their nestlings on rich and easily obtainable preys inhabiting near their nests.

The average of total feeding rate per day per nestling was 55.4 times in the White wagtail, being higher than that of the Japanese wagtail (42.8 times). It was probable that the quantity of food delivered in each time by the White wagtail’s pair was smaller than that by the Japanese wagtail’s pair. This is probably because the distance between the nest of the White wagtail and its feeding sites used frequently was shorter than that of the Japanese wagtail. And a general tendency was observed that wagtails brought a larger quantity of foods from far feeding sites than from near ones.

6. Faecal sac treatment

After the parents of the White wagtail fed nestlings, they paused in the nest before flying out. The nestling fed raised the rear end of its abdomen and exhausted a faecal sac. The parent immediately picked it up. The male flew out of the nest with it and dropped it in the air (only once observed that it was eaten when two nestlings defaecated without a break). The female ate it in the early nestling stage, but later she flew out of the nest with it and dropped as in the male (Table 4). The parent with faecal sac in its bill quickly flew out, but one without it landed on once and then flew out to gather foods after warning or preening. Male’s treatment of defaecation was low in the morning and increased in the afternoon (Fig. 10-a). Female’s treatment didn’t show marked increase. Feeding rate increased as nestling stage proceeded but defaecation rate decreased in the middle nestling stage (see Fig. 9). Male’s share of faecal sac removal was 28%.

The parent of the Japanese wagtail removed faecal sacs in the same way as the White wagtail. In both species females ate a faecal sac in the early stage and flew out with it in the late stage, but males flew out with it in their bills through nestling stage. De-

<table>
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faecation rate of the Japanese wagtail was high in the morning, when feeding rate was high (see Fig. 10-b). The ratio of defaecation to feeding was 1/4.3 in the White wagtail, which was lower than the Japanese wagtail (1/3.9) in this study area, but near to 1/4.4 in the Japanese wagtail studied by Haneda & Shinoda (1969).

Each parent of the Japanese wagtail laid down faecal sacs into the same water pool. Such behaviour was also reported in the Grey wagtail, Motacilla cinerea (Hasegawa 1976), but could not be confirmed in the White wagtail.

II. Growing up

1. Eggs and chicks

The five eggs in one brood of the White wagtail just after being laid were, on the average, 22.78 mm in long diameter, 16.44 mm in short diameter and 3.28 gram in fresh weight. The average egg sizes of 51 eggs of the Japanese wagtail just after being laid were 20.88 mm in long diameter, 16.38 mm in short diameter and 3.03 gram in fresh weight. As far as these data are concerned, the egg sizes of the White wagtail were a little larger than the Japanese wagtail, as well as three subspecies of Motacilla alba in Europe (M. a. yarrellii 20.56 × 15.29 mm, M. a. alba 20.4 × 15.1 mm, and M. a. personata 20.1 × 15.2 mm; Witherby et al. 1940).

Egg weights decreased through egg-laying and incubating stages (Fig. 11). The rate of decrease was almost constant, irrespective of brood or species. Unhatched
Breeding Ecology of *Motacilla aila* and *M. grandis* and their Interspecific Relationship

1. Change of egg weight.

Eggs decreased more sharply than hatched eggs. The rate of decrease just before hatching became sharper than before. Eggs in a brood hatched on the same day or within two days. This was dependent upon the start of full incubation, before or after completion of the clutch. The hatching order within a brood of the Japanese wagtail was equal to the laying order.

When a chick hatched, the female of both species ate its egg shell or flew out of the nest with it. Chick’s weights of the White wagtail in the hatching day were 2.32 gram on the average (n=3). Those of the Japanese wagtail just after hatching were 2.13 gram on the average (n=14).

2. Growth of nestling

In the fifth day after hatching the eyes of nestlings of the White wagtail opened, and they began to flap the wings in the tenth day, and fledged in the morning of the thirteenth day. From the hatching day to the fledging day, the body weight of nestling increased from 2.32 gram to 23.7 gram. From three days old to thirteen days old, its wing length grew from 14.4 mm to 63.8 mm and its leg length did from 8.4 mm to 23.9 mm (Fig. 12).

Fig. 13 shows the growth curves of the Japanese and the White wagtails in terms of body weight. These curves were well represented by the “sigmoid growth curve”. Initial increase in growth rate occurred a few days later in the White wagtail than in the Japanese wagtail, and this lag of time continued until the maximum size was attained. The ratio of nestling on the fledging day to adult was 89% in body weight, 67% in wing
Fig. 12. Growth curves of nestlings of White wagtail in averaged body weight, wing length and leg length. Open symbols show the averaged body weight, wing length and leg length of adults, respectively (After the banding data of the Yamashina Institute for Ornithology in 1977).

Fig. 13. Growth curves of averaged body weight of nestling in each brood of White and Japanese wagtails.

length, and 98% in leg length (see Fig. 12). The body weight and leg length of nestlings almost attained those of adults, but the wing length of nestlings was much shorter than that of the adult. Nestlings of the Chinese tree-pipit, *Anthus hodgsoni*, also fledged even when their wing length was 46% of adults (Haneda & Hasegawa 1970). Leg length may
be more important for nestlings of Motacillidae to fledge than wing length.

**III. Interspecific Relationship between the White wagtail and the Japanese wagtail**

Japanese wagtails exclude conspecific intruders of the same sex out of the song area (that is 'the occupied area') with extremely high aggressiveness (Nakamura 1982). While, the spatial relationship between song area and aggressive behaviours on the White wagtail has not been studied in detail. In this study we could not refer to these relations, because the conspecific encounters of the White wagtail were observed only seven times; five chasings and two mutual threatenings. It seems to be clear that the White wagtail shows territorial behaviours, however, as being suggested by other studies (Davies 1976 and 1981, Watanabe & Maruyama 1977 and Zahavi 1971).

A pair of the White wagtail and a pair of the Japanese wagtail bred while largely overlapping their home ranges in this study area (Fig. 14). Their nests were built closely to each other. So their encounters were frequent and aggressive behaviours were observed. Japanese wagtails were always aggressive towards White wagtails. All of 123 times chasings between them were those of Japanese wagtails to White wagtails (Table 5). These distributed over their whole home ranges, especially near their nests and foraging sites. White wagtails were always defeated by Japanese wagtails even at the sites where they chased the conspecific intruders. It was always the Japanese wagtail that was a chaser in the chasing-chased relationship. This fact was also suggested by Higuchi & Hirano (1983), who studied on wintering ecology of White and Japanese wagtails. Only once a male White wagtail opposed to a male Japanese wagtail which turned aggressive towards it. But it was the White wagtail that flew away after the physical combat.

The most aggressive chaser of the Japanese wagtail towards White wagtails was the male. Most of the chasings were those towards the male White wagtail. Chasings of the female Japanese wagtail occurred when her mate was absent within the area where he could catch the sight of White wagtails. When the male Japanese wagtail chased White wagtails, his mate was absent at the scene in the most cases. She participated in breeding works over the half of times when the male chased White wagtails (Table 6). A few occurrences of interspecific chasings between females might partly be attributable to the fact that they hardly encountered each other, and partly to the fact that a female Japanese wagtail accompanied with a mate was indifferent to a female White wagtail even in the immediate neighbourhood.

Japanese wagtails did not always chase White wagtails. The former was sometimes indifferent to the latter, even when the latter came within 10 meters from the former where both could probably witness each other (see Table 5). The male Japanese wagtail did not expel White wagtails in 8.1% of all encounters (chasings + encounters within 10 meters), and the female in 59.1%. In this respect, interspecific response of the Japanese wagtail to the White wagtail was different from the intraspecific response, since Japanese wagtails infallibly chased conspecific intruders.

Interspecific interaction may cause various influences to both species involved in it. In the case when one species is unilaterally aggressive towards the other species, the latter would suffer harmful influence.
S. Nakamura, H. Hashimoto and O. Sootome

Fig. 14. Home range and distribution of aggressive behaviours in White and Japanese wagtails. Home range of White wagtail is showed with minimum convex polygon including all observed points. (a) 1978. Broken and solid lines show home ranges of White and Japanese wagtails, respectively. Numbered triangles and circles are nest sites of Japanese wagtail. Numbered squares are nest sites of White wagtail. ●, ▲: chasings of male and female Japanese wagtails towards White wagtails, respectively. ■: chasing of male White wagtail towards conspecific intruders. (b) Combining the data in rice field in 1979 with those on the campus in 1980. Dotted broken and solid lines show home ranges of Japanese wagtail in 1979 and 1980, respectively. Broken line does the home range of White wagtail. N with a square shows the nest site of White wagtail, and the others do nest sites of Japanese wagtail. ○, ●: chasings of male Japanese wagtail towards White wagtails in 1979 and 1980, respectively. △: chasing of female Japanese wagtail towards White wagtails in 1979. ■: chasing of male White wagtail towards conspecific intruders in 1980. □: mutual threatening of male White wagtail.

Table 5. Combination frequency of chasing of Japanese wagtail to White wagtail.

<table>
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<tbody>
<tr>
<td></td>
<td></td>
<td>M</td>
<td>F</td>
<td>MF</td>
<td>N</td>
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</tr>
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<td></td>
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<td>68</td>
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<td>12</td>
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<tr>
<td>%</td>
<td></td>
<td>59.7</td>
<td>14.9</td>
<td>14.9</td>
<td>10.5</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Female</td>
<td>3 years</td>
<td>4</td>
<td>2</td>
<td>1</td>
<td>2</td>
</tr>
</tbody>
</table>

M: Male, F: Female, MF: Male and/or female, N: Nondistinctive, I: Indifferent within 10 m.
Breeding Ecology of *Motacilla alba* and *M. grandis* and their Interspecific Relationship

Table 6. Female behaviours when her mate chased White wagtail.

<table>
<thead>
<tr>
<th></th>
<th>Ab</th>
<th>Br</th>
<th>In</th>
<th>FW</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>1978</td>
<td>24</td>
<td>17</td>
<td>1</td>
<td>—</td>
<td>42</td>
</tr>
<tr>
<td>1979</td>
<td>—</td>
<td>28</td>
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<td>14</td>
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</tr>
<tr>
<td>Total</td>
<td>38</td>
<td>57</td>
<td>10</td>
<td>9</td>
<td>114</td>
</tr>
<tr>
<td>%</td>
<td>33.3</td>
<td>50.0</td>
<td>8.8</td>
<td>7.9</td>
<td>100</td>
</tr>
</tbody>
</table>

Ab: Female was absent at the scene and her behaviour unknown, Br: Female participated in breeding works, mainly incubation, In: Female was indifferent, FW: Female fed and walked.

This occurred in the repeated brood of the White wagtail in 1978. One day after the pair of the White wagtail began to lay eggs (May 24), the pair of the Japanese wagtail began the third nesting at a distance of 46 meters apart on the same building on the campus (May 25). Till then the male Japanese wagtail hardly stayed on the building (f), where the pair of the White wagtail had finished the first brood in failure (Fig. 15). Since the day when nesting began the male Japanese wagtail started to stay long time there. Consequently the encounter between the male Japanese wagtail and the male White wagtail increased. The former chased the latter whenever it approached its own nest. The male White wagtail scarcely incubated in the repeated brood, though it in-
cubated for 6% of the daytime incubation in the first brood on the average (Fig. 4), which was due to the fact that he could not approach the nest because of the aggression of the male Japanese wagtail. The pair of the Japanese wagtail abandoned their eggs on June 4, and began to construct the fourth nest on another building, so that the staying time of the male Japanese wagtail on the building formerly nested became very shorter. Then the male White wagtail could approach the nest. After his chicks hatched (June 8), when the Japanese wagtail’s pair had ceased breeding, he delivered food for them frequently at the nest.

Discussion

The breeding habits of the White wagtail showed the similar pattern to that of the Japanese wagtail; however contributions by the male White wagtail to daytime incubation and feeding were less than that of the male Japanese wagtail, and food for nestlings were different between the two species except for the most common items. Although the spatial relationship between their song area and aggressive behaviours hasn’t been elucidated in the White wagtails yet, it would be like that of the Japanese wagtails because both species took the similar aggressive behaviours (Zahavi 1971 and Nakamura 1982). The obvious behavioural difference between the two species, which has not been referred to in this paper, was the vocalization as mentioned in many literatures (Takano 1982 etc.). And there was a slight difference in the posture of the appeasement display; in the White wagtail the position of the waist was under the level of shoulder as shown in Zahavi (1971), while in the Japanese wagtail the position was over the level of shoulder as illustrated by Hirano (1981) and Nakamura (1982). It is unknown in practice what degree of difference in the reaction of the recipient these dissimilarities make. However, these differences seem to play some roles as the behavioural pre-mating isolation, which would prevented the two closely related species from crossing.

When a pair of closely related species comes into contact with each other as the result of extending their distributions, there is the potential for behavioural interaction and competition for resources. In this case it has been suggested that habitat segregation results from competitive exclusion. On the other hand, Murray (1971) suggested that habitat segregation occurred from interspecific territoriality; he assumed that interspecific territoriality was misdirected intraspecific territoriality and was nonadaptive.

The contact between the Japanese wagtail and the White wagtail as a result of the extension of the latter’s breeding range offers additive data to the above discussion. Japanese wagtails obviously dominated over White wagtails. The latter coped with the aggression of the former by means of flying away. But the aggressiveness of the Japanese wagtail towards the White wagtail was not so severe as that towards the conspecific wagtail, so that it could not thoroughly exclude the subordinate White wagtail. The White wagtail merely eluded the aggression of the Japanese wagtail and did not retreat from the area where it received the aggression from the Japanese wagtail. This suggests therefore that they don’t show interspecific territoriality to each other.

Because the Japanese wagtail had to some degree similar requirements for nesting site
and foods for nestlings as the White wagtail, the aggressiveness of the Japanese wagtail could be adaptive in that it could secure the resources by excluding the White wagtail. Taking account of the fact that the aggressiveness of the Japanese wagtail was incomplete, however, it could be regarded as the misdirected intraspecific territoriality or would have not been selected for yet. On the other hand it could sufficiently exert the harmful influence on the breeding of the White wagtail even with the incomplete aggressiveness. If this influence had come up to the nestling stage, the White wagtail would have suffered heavier influence incurring the decrease of foods for nesting. But the number of individuals on which is exerted this influence may be a few, because the area where the interaction between the two species occurs is a very small part in the overlapping area of breeding range of the two species. In fact, as mentioned in Higuchi & Hirano (1981), the home ranges of the two species in the breeding season would almost segregate each other. One-way aggressiveness of the Japanese wagtail could be regarded as a cause of the segregation of home range, or habitat segregation, in the overlapping area of their breeding ranges.

The harmful influence on the White wagtail could be avoided if its breeding season was one or two months later than that of the Japanese wagtail. This lateness of breeding season must be effective to reduce the competition between them (Higuchi & Hirano 1981). The breeding season of the Japanese wagtail extended into June and July in the area where the White wagtails bred, as in this study area, however, thus the lag of the initiation of breeding seasons does not seem to be so effective as to soften the aggressive interference of the Japanese wagtail towards the White wagtail. Rather, it may be accomplished by the segregation of their home ranges or the habitat segregation, viz., that the White wagtail bred finding their way into the area where the Japanese wagtail was absent, eluding the aggression of the latter by the lateness of the former’s breeding season.

The extension of breeding range of the White wagtail inland has proceeded covering factory areas and town areas. The Japanese wagtail also shows the tendency of colonization into there. After Haneda & Shinoda (1969), the nest site of the Japanese wagtail in the riverside was almost on the ground surface. When they used the habitat adjacent to town area for breeding, the Japanese wagtails built their nests on buildings. Nests of the White wagtail were almost built on buildings as well. Half nests of the Pied wagtail, Motacilla alba yarrellii, were also associated with buildings or similar structure in Britain (Mason & Lyczynski 1980). It seems to be reasonable that buildings are rather safe places for nesting sites in the town area and its outskirts. In addition to this, factory buildings, reinforced concrete buildings with the flat roof offer the many suitable sites for the nesting habit of wagtails, which builds a nest being put on the ground surface or in holes, clefs or ledges. As their habitats extend into the town area, they utilize cultivated lands and irrigation or drainage ditches at the periphery of them for foraging sites. Although such circumstances have been existent since before and have been sites for foraging sites, they were not used for breeding because they did not hold the suitable site for a nest. With the enlargement of town areas, the buildings offering nesting sites came into to closer contact with cultivated lands and ditches. Moreover the suitable space for walking feeding on the open land, which is one of the feeding characteristics of
wagtails, increased with the development of vegetable culture more than the previous single crop cultivated lands for only the paddy or the barley. Suspending cultivated land and construction area have also increased the similar space. Accordingly the town area and its circumference offer the new breeding habitat to wagtails on both sides of nesting site and feeding site. The extension of breeding range of the White wagtail seems to have proceeded corresponding to such changes. The degree of extension is thought to depend on the degree of similarity between the circumstances of town areas or such and the previous breeding circumstances or the adaptability to such environments. From these points of view it would be interesting to make a comparative study on the breeding habitat and the breeding ecology, especially nesting sites and foods, between the newly established breeding range and the old one. Interspecific relationship between the White wagtail and the Japanese wagtail also needs to be examined more quantitatively on the same comparison.

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References

Breeding Ecology of *Motacilla alba* and *M. grandis* and their Interspecific Relationship


ハクセキレイとセグロセキレイの繁殖生態と種間関係について

茨城県水戸市において、本州を含む繁殖地を南下拡張しつつあるハクセキレイと在来繁殖種であるセグロセキレイの繁殖生態を、両種の種間関係について調査した。

1. 市街地およびその周辺におけるハクセキレイの繁殖期は4月から7月であり、セグロセキレイのなかで同じ環境に繁殖する個体の繁殖期を大きく重複した。両種とも市街地周辺では建造物に営巢し、同じ巣場所を利用することもあった。

2. ハクセキレイ雄は繁殖仕事のうち、巣造りの8％、抱卵の6％、給餌の36％、糞処理の28％を分担した。このうち抱卵と給餌への貢献は、セグロセキレイ雄の貢献より少なかった。

3. 両種の雌への主要な餌グループの2つのうち1つは同じであり、ガガンポコであった。

4. 繁殖期を通じ、セグロセキレイはハクセキレイに対し力関係において明らかに優位であった。セグロセキレイのハクセキレイに対する攻撃性は、同種に対するように完全なものではなかったが、ハクセキレイの抱卵分担を減少するのに十分であった。この攻撃性は、両種の繁殖分布の重複部における生息地分離の一因となっていると考えられた。

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