Comparative Ecology of White and Japanese Wagtails, *Motacilla alba* and *M. grandis*, in Winter

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冬季におけるセグロセキレイとハクセキレイの比較生態

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The White Wagtail *Motacilla alba* is widely distributed throughout Europe and Asia, whereas the Japanese Wagtail *M. grandis* is endemic to Japan. The latter species is believed to be differentiated in geologically recent times from the former through geographic isolation (MAYR, 1963: 503). Until about the early 1970's the breeding ranges of the two species in Japan were generally separate but overlapped locally in Hokkaido and northern Honshu and in southern Kyushu. Recently however, the northern (*M. a. lugens*) and the southern (*M. a. leucopsis*) populations of White Wagtails are expanding their breeding areas into central Japan (NAKAMURA, 1978, HIGUCHI & HIRANO, 1981), thereby increasing sympatricity with *M. grandis*.

We have investigated the comparative ecology of the two species in Utsunomiya (36.5 N, 139.8 E), central Honshu, where *M. alba lugens* has established itself as resident since about 1976 and is thus secondarily sympatric with *M. grandis* (HIGUCHI & HIRANO, 1981). The two species occur in similar abundance in the river that was selected for our study area. This situation is suitable for observing the ecological relationships of the species, which tend to be segregated by habitat in other sympatric areas.

In the present paper we describe the pair duration, territoriality, habitat preference, and feeding technique of the two species in winter, and discuss the significance of the ecological differences. The ecology of these species has been studied by HIRANO (1981, *M. grandis*) and by WATANABE & MARUYAMA (1977, *M. alba*), but these authors were concerned only with the species individually.

STUDY AREA AND STUDY METHOD

Observations were made every two or three days from November 1981 to January 1982 along the Tagawa River in Utsunomiya City. The river is 30-50 m wide, and a

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sector of 2 km long was selected for the field work. About 90% of the river is open water, but dead twigs and water vegetation such as *Ranunculus* and *Hydrilla* emerge from the water as islets and provide the wagtails with feeding areas. The rest is chiefly gravelly areas. Grasses are found in some places along the riparian bank, which is made of concrete. Beyond the bank are paddy fields, farmland, and human habitation.

The positions and behaviour of individual wagtails were recorded on a 1:1,500 scale map. The boundaries of territories were confirmed only on the river, based on the points where aggressive behaviour was observed. In some territories, the position of individuals was plotted every three minutes to determine the intensity of use in different parts of the territory. This investigation was conducted for periods of one hour per territory, and a total of 6–8 hours were spent for each territory. Time spent on the river by individual wagtails and frequencies of aggressive behaviour were also investigated for periods of one hour per territory or individual.

No individuals were ringed, but it was possible to recognize individual wagtails by differences in plumage pattern and other morphological features including bill colour and leg injury. The difference of plumage pattern was particularly noticeable in *M. alba* and all the individuals on the river were easily identified. In *M. grandis* individual recognition was more difficult. Consequently individuals observed in particular sections of the river were considered to be the same individuals unless some difference of plumage or behaviour was noted. The sexes were also distinguished by plumage pattern in both species. In *M. grandis* the colour of the back is darker in males than in females (YAMASHINA, 1933). For *M. alba*, those individuals having a black head and large black bib were considered to be males and the others females. This distinction of sex in *M. alba* was confirmed, at least in our study area, by continued observations extending into the breeding season.

The feeding technique of wagtails was classified into the following four categories. (1) Ground feeding: feeding on the ground, concrete banks, or house roofs while walking; (2) flycatching I: feeding on insects in the air above the water surface; (3) flycatching II: feeding while flying at the water surface; (4) flycatching III: feeding on insects on the walls of banks and buildings while flying. The frequency of these different feeding techniques was investigated by counting the number of capture attempts for one minute repeated 2–4 times a day, for each individual.

Body sizes were measured in relation to feeding technique. The measurements of wing, bill, and tail were obtained from wild birds captured in Utsunomiya City in 1978–1982, and from specimens in the Yamashina Institute for Ornithology. Body weights were obtained only from the wild birds. The sexes of *M. alba* were not distinguished when the wild birds were measured.

RESULTS

(1) Pair duration and territoriality

Thirteen territories of *M. grandis* (A–M) and 10 of *M. alba* (i–x) were observed in our study area (Figs. 1–2). The territories of the two species greatly overlapped and interspecific territoriality was not observed in the study area. Actually, in at least

Fig. 1. The distribution of territories of *M. grandis* and *M. alba* in the study area in mid-December 1981. The broken line between territories iii and iv of *M. alba* indicates that the boundary is uncertain due to the lack of aggressive behaviour.

six locations the two species had territories whose extent and boundaries nearly concided.

The territories of *M. grandis* were occupied by pairs except for one or two which were occupied by single males. These territories remained unchanged from November to January, except that territory M was vacated by the pair in late December and was invaded by the male of neighbouring territory L. Pair relationships also seemed to be unchanged during the study period except that the female of territory E disappeared in early January (Fig. 2). The boundaries of the territories were sharply defended by ritualized aggressive behaviour (cf. HIRANO, 1981) and there were few intrusions into occupied territories.

Fig. 2. Periods of residence and pair duration in *M. grandis* (above) and *M. alba* (below) in the study area. An arrow in territory ii of *M. alba* indicates the displacement of the male after the disappearance of the male of territory iii.

M. alba differed from *M. grandis* in territorial condition. Only 3 or 4 of the 10 territories were occupied by pairs and the rest were occupied by single males. Moreover, the pair bond was temporary and maintained for only 25 days or so in the pairs of territories v and ix (Fig. 2). In these apparent pairs, it was the females that disappeared from the territories. The boundaries of the territories were not always clear in this species. For example no aggressive behaviour was observed near the boundary between territories iii and iv. Some floating individuals were also found.

(2) Use of the river

The time spent in the territories on the river was much longer in *M. grandis* than in *M. alba* (Table 1, Mann-Whitney $U=1$, $P<0.01$). *M. grandis* spent on an average 52.3 (males) and 53.9 (females) minutes per hour on the river, whereas *M. alba* spent only 30.3 (males) and 36.7 (females) minutes. Both species spent more than 90% of

Table 1. Time spent by *M. grandis* and *M. alba* on the river.

Territories investigated	Sex	Hours of observations	Time(min.) spent on the river	Time(min.) spent on the river per hour
<i>M. grandis</i>				
A	♂	7	326	46.57
	+	2	118	59.00
B	♂	6	299	49.83
	+	3	174	58.00
E	♂	7	396	56.57
I	♂	8	473	59.13
J	♂	8	371	46.38
	+	8	351	43.88
K	♂	8	443	55.38
	+	8	437	54.63
<i>M. alba</i>				
i	♂	7	128	18.29
ii	♂	7	128	18.29
iii	♂	5	176	35.20
	+	2	91	45.50
vii	♂	8	252	31.50
viii	♂	8	287	35.88
	+	6	204	34.00
ix	♂	8	341	42.63
	+	4	122	30.50

their time on the river for feeding. Away from the river, *M. grandis* perched mainly on the buildings nearby, but *M. alba* often went further.

Although the territories of the two species overlapped to a great extent, the main feeding sites seemed to be segregated from each other. The frequency of use of different parts of territories were investigated in four territory pairs (A-i, I-vii, J-viii, K-ix) in which the territorial boundaries of the two species were largely superimposed on each other except for the north boundary of territory vii (Fig. 3). We considered the difference between territories I and vii unimportant since the northern segment of vii was little used. In three of these four territory pairs, activity centers or the main feeding sites of the two species were segregated. In territory pair I-vii the segregation was not so evident as in the other three. However, in this situation the individuals of the two species rarely fed close together; individual distances of more than 50 m were maintained during most feeding activities.

Chasing between the individuals of the two species was often observed. *M. grandis* always chased *M. alba* regardless of the sexes and never vice versa. When *M. alba* approached *M. grandis* too closely, the latter slightly repulsed the former. Then *M. alba* would fly away a few meters and continue to feed. In such cases, *M. alba* did not show the appeasement behaviour toward *M. grandis*, which is displayed by the conspecific female or subordinate juvenile toward the male in both *M. alba* (ZAHAVI, 1971, WATANABE & MARUYAMA, 1977, DAVIES & HOUSTON, 1981) and *M. grandis* (HIRANO, 1981). When *M. grandis* moved toward *M. alba*, the former was not chased by the latter. Instead, even in the latter's activity center, *M. grandis* chased *M. alba*.

Table 2 shows the frequency of chasing as observed in the four territory pairs dis-

Table 2. Frequency of chasing of *M. alba* by *M. grandis* in territories with similar interspecific boundaries.

Chasing toward	Hours of observations	No. of chases observed	No. of chases per hour
A ♂→i ♂	6	7	1.17
A ♀→i ♂	6	6	1.00
I ♂→vii ♂	7	75	10.71
J ♂→viii ♂	8	13	1.63
J ♂→viii ♀	8	15	1.88
J ♀→viii ♂	8	4	0.50
J ♀→viii ♀	8	7	0.88
K ♂→ix ♂	6	4	0.67
K ♂→ix ♀	5	7	1.40
K ♀→ix ♂	6	20	3.30
K ♀→ix ♀	5	15	3.00

Table 3. Use rates of the four types of feeding technique in *M. grandis* and *M. alba*. See study method for the explanation of flycatching I-III.

	<i>M. grandis</i>	<i>M. alba</i>
Total capture attempts observed	6172	3287
Feeding technique (%)		
ground feeding	96.9	92.7
flycatching I	2.4	5.0
flycatching II	0.7	2.3
flycatching III	0.1	0.0

Table 4. Use rates of the two types of ground feeding places in *M. grandis* and *M. alba*.

	<i>M. grandis</i>	<i>M. alba</i>
Total capture attempts observed	5978	3047
Feeding place (%) water edge and shallow water	65.7	37.0
sand, gravel, and banks	34.3	63.0

cussed earlier. An individual of *M. alba* was chased by an individual of *M. grandis* on an average of 1–3 times an hour in the three territory pairs. In territory pair I–vii, where the segregation of feeding sites was not clear, there were about 11 chases per hour and the chasing was more aggressive than in the other cases.

(3) Feeding technique

Both species used ground feeding more frequently than flycatching. Flycatching I, II, and III were used in decreasing order of frequency (Table 3). There were slight differences of feeding technique between the two species, i.e. *M. grandis* used ground feeding significantly more often and flycatching less often than *M. alba* ($\chi^2=84.32$, 1df, $P<0.001$). A remarkable difference was found between the two species in their ground feeding sites (Table 4). *M. grandis* fed more often at the water edge or in shallow water; *M. alba* fed more often in drier areas such as on sand, gravel, and banks ($\chi^2=676.43$, 1df, $P<0.001$).

Fig. 3. Activity densities of *M. grandis* (above) and *M. alba* (below) in the territories whose boundaries are similar in the two species. Shading in the grid is based on percentage of observation points, counted once every three minutes, falling in the respective quadrats. Territory symbols are the same as in Fig. 1.

Fig. 4. Body weight in relation to wing length in *M. grandis* (●: male, ○: female) and *M. alba* (▽: sex unknown). All data used are taken from captured wild birds; data from specimens are not included because they lack body weight data.

(4) Body size

The wing and tail lengths are longer in *M. grandis* than in *M. alba* in females, but not in males (Table 5). The body weight tends to be lighter in relation to the wing length in *M. alba* (Fig. 4). That is, the body of *M. alba* tends to be more slender than that of *M. grandis*. The beak is shorter and thicker in *M. alba* than in *M. grandis* (Table 5 and Fig. 5). The ratios of *M. grandis* to *M. alba* in mean culmen length and beak height were 1.08 and 1.08 for males, and 1.05 and 1.10 for females.

DISCUSSION

M. alba spent less time on the river than *M. grandis*. This suggests that *M. alba* is less dependent on the river. Since *M. alba* sometimes go far away from the river, the territory on the river may be only a small part of the whole territory or home range in

Table 5. Comparison of body sizes of *M. grandis* and *M. alba*. Data were from both the wild birds captured and preserved specimens. Measurements in mm.

		<i>M. grandis</i> Mean±S.E. (N)	<i>M. alba</i> Mean±S.E. (N)	<i>t</i>	Significance level
Wing length (flattened)	male	96.21±0.42 (38)	96.58±0.55 (20)	0.53	n.s.*
	female	92.73±0.33 (35)	89.93±0.89 (7)	2.95	<i>P</i> <0.01
Tail length	male	99.33±0.43 (38)	98.30±0.50 (20)	1.56	n.s.*
	female	94.97±0.58 (35)	92.29±0.92 (7)	2.46	<i>P</i> <0.05
Culmen from the skull	male	19.06±0.12 (21)	17.70±0.17 (21)	6.54	<i>P</i> <0.001
	female	18.41±0.14 (8)	17.49±0.17 (8)	4.18	<i>P</i> <0.001
Beak height at anterior edge of the nostril	male	3.62±0.04 (21)	3.90±0.04 (21)	4.91	<i>P</i> <0.001
	female	3.46±0.05 (8)	3.81±0.06 (8)	4.49	<i>P</i> <0.001

* n.s.=not significant (*P*>0.05)

Fig. 5. Relation of beak height to culmen length in *M. grandis* (●: male, ○: female) and *M. alba* (▲: male, △: female, ▽: sex unknown). Data from both the wild birds captured (sex unknown in *M. alba*) and from the preserved specimens.

this species. WATANABE & MARUYAMA (1977) also suggested that *M. alba* occupants of territory on the river have one or more feeding areas outside the river. Such habits probably are related to the fact that some individuals of *M. alba* loosely defend the territory boundaries on the stream. The tendency to wander over a wide range may also explain the unstable pair relationship and the presence of floating individuals.

M. grandis, on the other hand, depends largely on the river and the territory on the river is the center of its life. The boundaries of territories are therefore defended more sharply in this species. The stable pair relationship is also significant in this context, although HIRANO (1981) reported that the pair mates were sometimes changed in early spring.

It seems important that some of the territory boundaries are close to each other in the two species. However, it is not clear what the cause is. The boundaries did not coincide with any apparent topographical or other physical feature of the environment. Since *M. grandis* is the dominant species, *M. alba* may be in the territory of *M. grandis* as a kind of "satellite", as described by DAVIES & HOUSTON (1981) for a conspecific female or juvenile subordinate in the territory of *M. alba*. One advantage which may have in such a situation is that *M. grandis* sometimes defends the territory against *M. alba* of neighbouring territories.

Although the territories on the river overlapped to a great extent between *M. grandis* and *M. alba*, the activity centers were clearly segregated, and individual distances apparently were maintained between the two species. No doubt such spacings are brought about by *M. grandis* chasing *M. alba*. This chasing was not so belligerent as the repelling of conspecific intruders by the territory occupants. However the frequency of 1-3 times an hour on an average could be effective enough to space out the

neighbouring individuals. The activity centers of *M. grandis* were not considered to be superior to those of *M. alba* for feeding or defence from enemies. The reason the activity center was not clearly segregated in territory pair I and vii may be that only the male of each species occurred there. It might be easier for a single bird to enter the activity center of another single bird. The large area of non-overlapping in these territories cannot be considered the reason for the obscure segregation of their activity centers, since feeding in the non-overlapping area is rare.

Feeding competition between the two species could be greatly reduced by a difference in degree of dependence on the stream and spacing out of individuals between the two species. There is also a definite difference in the place of the ground feeding, the most often used feeding technique in both species. *M. alba* apparently prefers drier areas and is inclined to leave the river more often than *M. grandis* to go to distant areas without water.

Although differences in the four types of feeding technique were small, all three types of flycatching were more often used by *M. alba* than *M. grandis*. The body of the former tends to be more slender than that of the latter. The slender body is perhaps more suitable for flycatching, though *M. alba* does not have the longer tail of those wagtail species which do more flycatching (DAVIES, 1977). These differences between the two species in the feeding place and technique suggest some segregation of their food, which is also suggested in the difference in bill size.

Nevertheless, the differences in feeding habits and morphology seem too small for the two species to coexist along the same river. The beak ratios of *M. grandis* to *M. alba* are much less than 1.3, which is considered to be the least value for difference in the feeding apparatus of closely related species inhabiting the same environment (HUTCHINSON, 1959). In fact, there are few river or other environments where these two species occur in similar abundance. As our results would predict, *M. alba* tends to prefer drier places such as cultivated lands and open factory areas, or rivers near the sea coast, while *M. grandis* is much more restricted to inland rivers (personal observations). We think that the reason why our stream has an abundance of both species may be the high productivity of the stream. We did not investigate that, but the greenish or brownish water colour suggested high productivity. Anyway, we are fortunate to have such a study area where the two species occur in similar abundance, an ideal situation for observing their ecological relationships.

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SUMMARY

(1) The territoriality, pair duration, and feeding habits of two species of wagtails, *Motacilla gandis* and *M. alba*, were studied in winter along a river in Utsunomiya, central Honshu.

(2) Territories of the two species overlapped each other to a great extent. In some cases the territorial boundaries of the two species nearly coincided with each other, but their activity centers tended to be located in different parts of the shared territory.

(3) *M. grandis* lived mostly in pairs, whereas many individuals of *M. alba* lived singly. The boundaries of territories were distinct in *M. grandis* but often vague in *M. alba*.

(4) *M. grandis* spent much more time on the river; *M. alba* sometimes went far away from the river. The greater dependence of *M. grandis* on the river was considered to be linked with the sharp defence of territory and stable pair duration.

(5) The difference in feeding technique between the two species was small. However, there was a significant difference in the places preferred for ground feeding, the technique most often used by both species.

摘 要

(1) 宇都宮市内を流れる田川で、1981年11月から1982年1月にかけての3か月間、セグロセキレイとハクセキレイの生態を調査した。

(2) 両者はそれぞれテリトリーをかまえて生活していたが、2種のテリトリーは種間テリトリーの様式をとらずに、完全に重複していた。しかも、いくつかのテリトリーでは、境界が2種でほぼ一致していた。ただし、そのような場合、2種がよく利用する空間は、テリトリー内で分離している傾向があった。

(3) セグロセキレイは大部分がつがいで生活していたが、ハクセキレイは多くが1羽でくらしていた。テリトリーの境界は、セグロセキレイでははっきりしていたが、ハクセキレイでは必ずしもそうではなかった。

(4) 川原で過ごす時間はセグロセキレイの方が明らかに長く、ハクセキレイはしばしば川原から遠く離れたところに飛んでいった。セグロセキレイが河川に強く依存していることと、そこにかまえたテリトリーをしっかりと守ることとの間には関連があるように思われた。

(5) 2種間の採食方法に見られる違いは、わずかなものであった。だが、両者が最もよく行なう地上採食のさいの利用場所には、はっきりとした違いが認められた。セグロセキレイはより水辺で、ハクセキレイはより乾燥したところで採食する傾向があった。

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