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Foraging niches of introduced Red-billed Leiothrix and native species in Japan

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ORNITHOLOGICAL SCIENCE

Abstract In Kyushu, southwestern Japan, the introduced population of the Red-billed Leiothrix *Leiothrix lutea* has increased rapidly and its range expanded considerably since early 1980s. In order to clarify the influences of Red-billed Leiothrix on native bird species, we examined the similarities and differences in foraging patterns among species occurring in a deciduous broadleaved forest on the Ebino Plateau, during the breeding seasons from 1997 to 2000.

Leiothrix foraged in a lower vegetational layer with bamboo, intermediate in height between the foraging levels of the Japanese Bush Warbler *Cettia diphone* and various *Parus* species. Foraging height, extent of foraging on deciduous trees and foraging technique were major factors best distinguishing Leiothrix from native species. Segregation of foraging niche was distinct and no apparent niche shift, due to invasion of the new species, was detected. Aerial insects tended to be more abundant just above bamboo, mainly about one meter above the canopy, than above bare ground. Thus, jumping, a specific technique used by Leiothrix, is effective for capturing aerial insects or agile invertebrates resting on leaves and twigs. Aerial insects were found to be abundant in the foraging space preferred by Leiothrix. Gleaning and hanging, techniques mainly used by native species, are suitable for capturing prey of low mobility such as Lepidoptera larvae. Probably due to morphological constraints, *Parus* spp. and Japanese Bush Warblers seldom foraged by jumping, indicating that they exploit quite different food resources from those utilized by Leiothrix despite their foraging spaces overlapping to some extent.

In the deciduous broadleaved forests of Kyushu, an avian guild of foraging aerial insects in intermediate and lower layers of the forests is poor. Such a community may be subject to the successful invasion of the Red-billed Leiothrix into native forests.

Key words Ecological isolation, Foraging niche, Interspecific competition, Introduced birds, *Leiothrix lutea*

The Red-billed Leiothrix *Leiothrix lutea*, originally occurring from southern China to the western Himalayas (Ali & Ripley 1972; Long 1981; Lever 1987; MacKinnon & Phillipps 2000), has been introduced to Japan where many naturalized populations have been found in deciduous broadleaved forests in central and southwestern Japan since the early 1980s (Tojo 1994; Eguchi & Amano 2000). The expansion of its range and the increase in its numbers has been particularly remarkable in Kyushu, southwestern Japan (Eguchi & Amano 2000). Where it is indigenous, the Red-billed Leiothrix occurs in various habitats including deciduous broadleaved forests, bamboo thickets, tea plantations, and secondary forests near human habitations from 900 m to 3,000 m asl (De Schauensee 1984; Long 1987). In Japan, Leiothrix inhabits deciduous broadleaved forests with a dense understory of dwarf bamboo, and utilizes low layers of forest vegetation (Eguchi & Masuda 1994). In Kyushu, the habitat of Leiothrix overlaps that of a number of native species including the Japanese Bush Warbler *Cettia diphone*, Long-tailed Tit *Aegithalos caudatus* and various *Parus* species such as the Great Tit *Parus major*, Coal Tit *P. ater*, Varied Tit *P. varius*, and Willow Tit *P. montanus* (Eguchi & Masuda 1994). These native species also occur widely in deciduous broadleaved forests in Japan (Nakamura

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1970, 1978).

Introduced birds may diminish the number of native species through interspecific competition (Mountainspring & Scott 1985; Jones 1996). Usually introduced bird species succeed in establishing self-maintaining populations only in habitats disturbed by people (Case 1996) where they compete only with introduced species (Moulton & Pimm 1983; Moulton 1993) The Red-billed Leiothrix has, however, invaded native forests in Japan and has increased rapidly in number. As a result of this, interspecific competition between Leiothrix and native species is likely in Japan.

Instances of interspecific competition are difficult to detect (Lodge 1993). One approach to clarifying such competition is the study of habitat selection (Sol et al. 1997). If competition exists, two major resources, nest-sites and food, may be limiting. Amano and Eguchi (2002) revealed differences in nest-site characteristics between the Red-billed Leiothrix and Japanese Bush Warbler in forest, and suggested that competition between them for nest-sites did not exist, however, no quantitative evaluation has so far been made of either their food resources or their foraging spaces.

Foraging niches are highly segregated among sympatric Paridae (Gibb 1954; Hogstad 1978; Morse 1978; Nakamura 1970, 1978; Ogasawara 1970, 1975). Such segregation is partly derived from interspecific competition (Lack 1971). The Willow Tit, for example, often shifts its foraging height when it occurs in mixed-species flocks in the presence of dominant Great Tit (Alatalo 1981). Niche shift, in the presence of competitive species, has also been observed in another Paridae community with a different species composition (Herrera 1978). Thus a shift of foraging location is important evidence of interspecific interference competition.

In this paper, we aim to clarify the patterns of foraging space and foraging techniques of the introduced Red-billed Leiothrix and of several sympatric native forest bird species. In addition, we will show Leiothrix utilizes a unique foraging space that native species rarely use.

STUDY AREA AND METHODS

1) Study area

The study was conducted from April to September during each breeding season from 1997 to 2000, on the Ebino Plateau, southwestern Kyushu, Japan (1,200 m in elevation; 31°56′N, 130°51′E). The study area was situated in a mixed forest (16 ha) composed of *Abies firma*, *Tsuga sieboldii*, *Pinus densiflora*, *Quercus crispula*, *Hydrangea paniculata*, *Symplocos coreana*, and *S. myrtacea*. The shrub layer was dominated throughout the forest by the dwarf bamboo *Sasamorpha borealis* (ca. 2 m in height). Only small patches of ground were bare. A road, approximately 10 m wide ran through the forest. The annual mean precipitation exceeds 5,000 mm on the Ebino Plateau, of which more than one-third occurs during June and July (data from Miyazaki Branch, Weather Service of Japan).

The Red-billed Leiothrix was first recorded in this area about twenty years earlier (N. Kamitanigawa pers. comm.). This species breeds from April to September and emigrates to lower areas for the winter (pers. obs.). During the breeding season, six resident native species regularly occur in the same habitat as Leiothrix; four Paridae (Great, Varied, Willow, and Coal tits), Long-tailed Tit, and Japanese Bush Warbler (see Appendix 1 for the morphological characteristics of these species). Other sympatric species, including two trunk-specializing foragers (Japanese Pygmy Woodpecker *Dendrocopos kizuki* and Nuthatch *Sitta europaea*), and one sallying forager (Blue-and-white Flycatcher *Cyanoptila cyanomelana*), were excluded from the analysis, because of their low abundance, scarcity of observations, or great difference in foraging techniques from Leiothrix.

2) Observation of foraging birds

We searched for birds as we walked along forest paths. When we encountered birds foraging, we recorded the following information: species, time of day, foraging height, height of trees on which birds foraged, foraging location, foraging technique and whether or not there was a dwarf bamboo understory beneath/around the foraging location. We compared the percentage occurrence of foraging above or inside dwarf bamboo, because small patches of dwarf bamboo and of bare ground are abundant in the study area. We divided foraging location into six categories: foliage (including leaf, flower, fruit, bud and twig), branch, trunk, undergrowth (defined as shrubs if they were 2 m tall or shorter), ground, and air. Foraging techniques were defined as follows: (1) glean, a technique in which a prey item was picked up from a substrate by a standing or walking bird; (2) jump, a technique in which a bird jumped upon a prey item and snatched it from a substrate; (3) hang, a technique in which a bird hanging on a substrate picked a prey item; (4) hover, a technique in which a hovering bird picked a prey item from a substrate; (5) hawk, capturing an aerial prey item in the air; (6) peck, a technipue in which a bird pecked a substrate and picked a subsurface prey item; and (7) others, other miscellaneous techniques were includeed. Heights were estimated to the nearest meter.

We followed individual birds as long as they remained in sight, because the foliage was dense and visibility in the forest was poor. We changed individuals after one foraging record had been collected. If only single birds or pairs were present, we collected two further foraging records from each bird once they had changed foraging trees or foraging locations. No more than one record was collected for an individual while in the same tree.

Observations were made from 0830 to 1700. For the analyses, data were pooled for all individuals of each species, for all months and years.

3) Measurement of abundance of invertebrate prey

We compared the abundance of aerial insects between areas above dwarf bamboo and areas away from dwarf bamboo. In May 1997, we set 500-ml aluminum cans daubed with sticky glue 3–4 m above the ground as traps. Pairs of traps were set, one of each pair was set above dwarf bamboo and the other was set 10 m away, and away from dwarf bamboo (Fig. 1a). In total, 50 pairs of traps were distributed throughout the study area. Two days after setting them, we recovered the traps and collected, and counted, all the invertebrates stuck to their surfaces. In 2000, in order to assess the vertical distribution of aerial insects above dwarf bamboo, we set sticky traps (commercial sticky fly traps; 70×3.5 cm) 3 m and 6 m above the ground, and 1 m and 4 m above the canopy of dwarf bamboo (Fig. 1b). These traps were set at 15 points for two days. Then, after recovering them, we counted the numbers of invertebrates on each trap. These invertebrates were identified either to the family or order level and divided into two size classes; larger than 5 mm but smaller than 10 mm, and 10 mm or larger.

RESULTS

1) Foraging height and tree height

There were significant interspecific differences in foraging heights at which birds foraged ($F_{6,829}$= 12.67, $P<0.0001$, ANOVA, Fig. 2). The Red-billed Leiothrix foraged mainly 4 ± 2 m (median and 25–75% percentiles) above the ground, and the Japanese Bush Warbler foraged mainly 3 ± 2 m above the ground, although the difference between these two species was not significant ($P=0.23$, Scheffè's test). The Varied Tit and Coal Tit frequently foraged in the upper layer of the forest above 8 m, significantly higher than Leiothrix ($P<0.001$ for each comparison, Scheffè's test). There were no significant differences in foraging height, however, between Leiothrix and Long-tailed Tit ($P=0.97$, Scheffè's test),

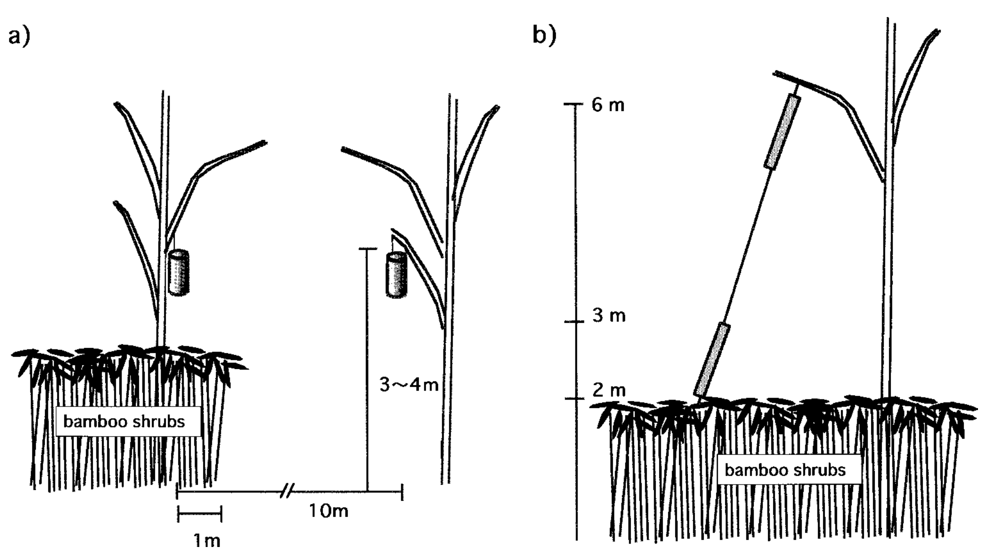

Fig. 1. Traps for collecting aerial insects. a) 500 ml can traps daubed with sticky glue, b) sticky ribbon traps (70×3.5 cm) set at 1 m and 4 m above a canopy of bamboo shrubs.

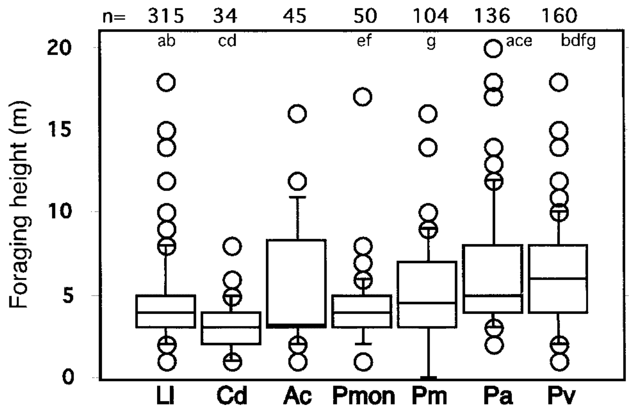

Fig. 2. Foraging heights of each species. Ll, *Leiothrix lutea*; Cd, *Cettia diphone*; Ac, *Aegithalos caudatus*; Pmon, *Parus montanus*; Pm, *P. major*; Pa, *P. ater*; Pv, *P. varius*. Crossbars represent 50% (median), boxes 25–75% percentiles and bars 10–90% percentiles. Circles are outliers. Pairs of a same character indicate a significant difference; a $P<0.001$, b,c,d $P<0.0001$, e,f $P<0.01$, g $P<0.05$, using Scheffè's F test.

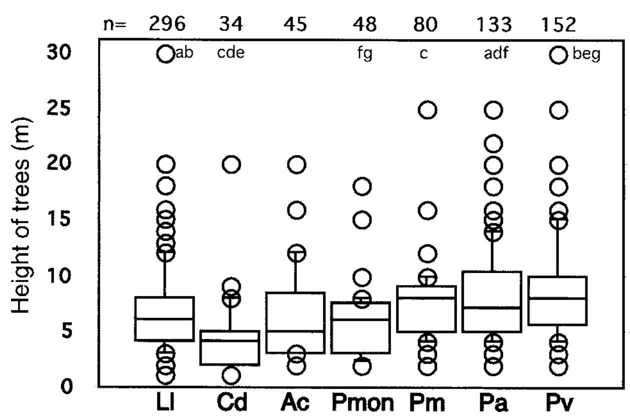

Fig. 3. Heights of trees in which each species foraged. See Fig. 2 for abbreviations. Pairs of a same character indicate a significant difference; a,g $P<0.01$, b,e $P<0.0001$, c,f $P<0.05$, d $P<0.001$, using Scheffè's F test.

Willow Tit ($P=0.98$) or Great Tit ($P=0.98$).

There were significant differences among bird species in the height of trees in which they foraged ($F_{6, 788}=10.90$, $P<0.0001$, ANOVA, Fig. 3). Japanese Bush Warblers mainly used trees or shrubs lower than 5 m. Varied and Coal tits used trees that were significantly higher than those used by Leiothrix ($P<0.0001$ and $P<0.01$, respectively, Scheffè's test). There were no significant differences, however, between the heights of trees selected by Leiothrix and the remaining species ($P=0.20$ Japanese Bush Warbler; $P=1.00$ Long-tailed Tit; $P=0.89$ Willow Tit; and $P=0.98$ Great Tit; all Scheffè's test).

2) Foraging location

The Red-billed Leiothrix, as well as the other species, mainly foraged in deciduous broadleaved trees, while Long-tailed Tits and Coal Tits also frequently foraged in coniferous trees (Fig. 4a). Japanese Bush Warblers often foraged in the undergrowth, mainly in dwarf bamboo.

Variation in foraging location was rather small (Fig. 4b). Each species foraged in foliage, mainly from leaves and twigs. In substrates other than foliage, Japanese Bush Warblers, Willow, and Great tits often foraged in the undergrowth or on the ground, while Coal and Varied tits foraged on branches and trunks. Great Tits also frequently caught prey in the air (aerial catching).

Both Red-billed Leiothrix and Japanese Bush Warbler exclusively used that part of the forest where there was dwarf bamboo in the understory, while the levels of occurrence in such areas was relatively low for the Long-tailed and Great tits, and intermediate for Willow, Coal, and Varied tits (Table 1). The overall difference was significant among species ($df=6$, $\chi^2=150.5$, $P<0.0001$).

3) Foraging technique

Species varied considerably in their foraging techniques (Fig. 4c). The major technique used by each species was gleaning. Red-billed Leiothrix, however, often foraged by jumping on prey items. Hanging was used frequently by Long-tailed, Willow, Coal, and Varied tits. Willow Tits and Coal Tits often pecked at buds and flowers, and also picked prey items. Great Tits also caught aerial insects gathering around flowers before leafing out in spring, whereas Japanese Bush Warblers foraged exclusively by gleaning.

4) Vertical distribution of invertebrates

From the results referred to above, it is clear that the Red-billed Leiothrix mainly used the lower layer of the forest with dwarf bamboo in the understory and it foraged more frequently by jumping than any of the other species. Foraging by jumping may be an effective technique for catching aerial insects resting on leaves or twigs. Leiothrix often foraged just above dwarf bamboo. Although there was no significant difference in the abundance of small invertebrates (5–10 mm), large Mecoptera, a dominant taxon among large ($\leq$10 mm) invertebrates (and eaten by Leiothrix,

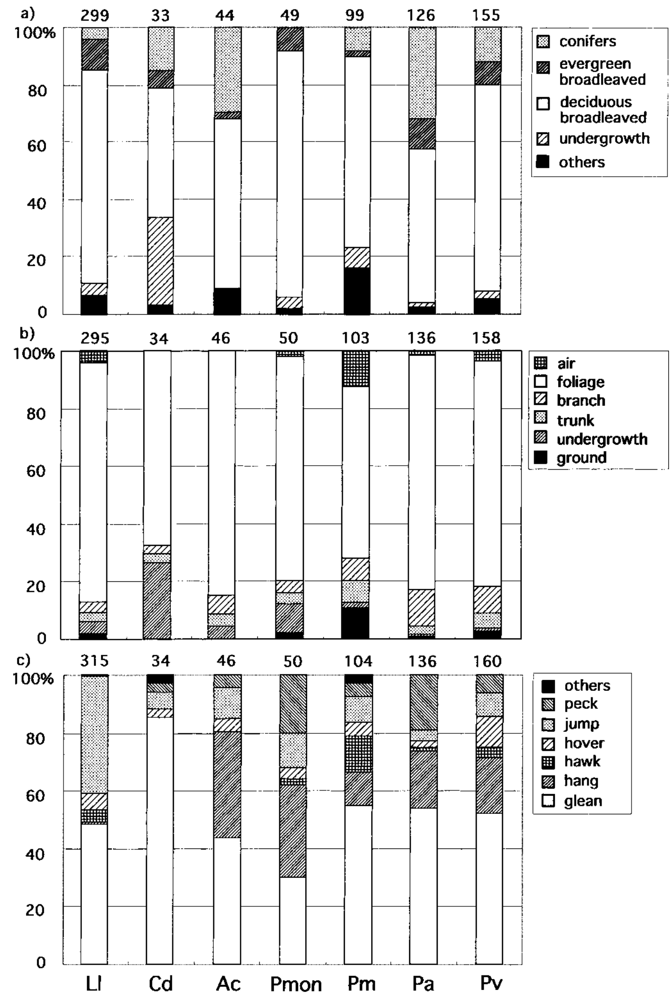

Fig. 4. a) Use of trees by each species, b) use of substrates by each species, c) foraging techniques used by each species. Figures above columns are the numbers of observations. See Fig. 2 for abbreviations.

Table 1. Percent occurrence of foraging above or inside of bamboo shrubs.

	Leiothrix lutea	*Cettia diphone*	*Aegithalos caudatus*	*Parus montanus*	*Parus major*	*Parus ater*	*Parus varius*
Yes	89.2	88.2	36.6	66	40.8	60.3	63.3
No	10.8	11.8	63.4	34	59.2	39.7	36.7
No. of observations	295	34	41	50	103	136	158

pers. obs.), were more abundant just above dwarf bamboo shrubs than above bare ground (0.44 ± 1.07 vs. 0.12 ± 0.39; mean number$\pm$SD; $N=50$, $P=0.048$, Wilcoxon signed rank test).

In a comparison between the abundance of invertebrates in an upper layer (4 m above dwarf bamboo canopy) and a lower layer (1 m above dwarf bamboo), the total abundances of both small and large invertebrates were greater in the lower level than in the upper in each month, but not significant (see Fig. 5). The only exception was for the abundance of small invertebrates in May (Fig. 5a). At taxonomic levels, the abundances of invertebrate in the lower layer also tended to be greater than in the upper layer, but the

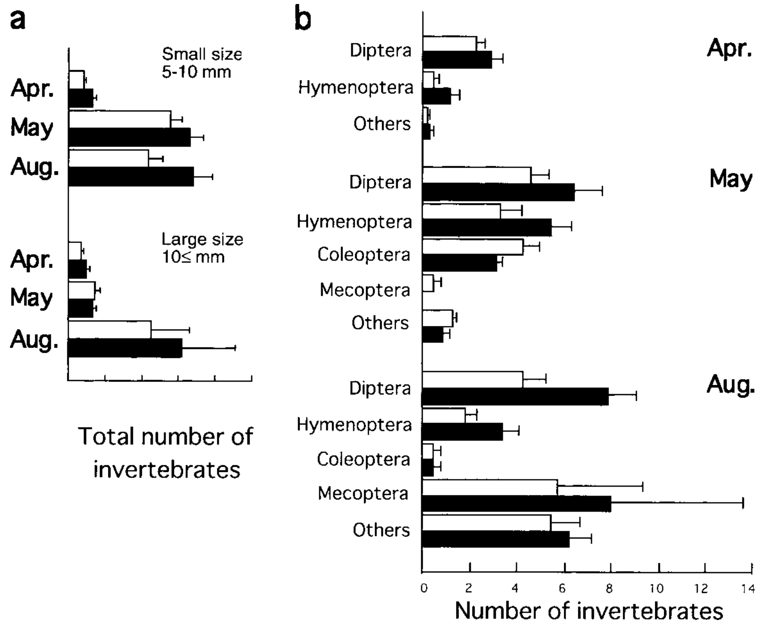

Fig. 5. Abundances of invertebrates (mean±SE) collected with sticky ribbon traps. a) the total numbers; b) the number of each taxon. Open bars and solid bars indicate upper traps and lower traps, respectively. See text for results of statistical tests.

differences were not significant (Wilcoxon signed rank test with sequential Bonferroni modification for multiple tests; Fig. 5b).

DISCUSSION

1) Differences in foraging patterns

In this study, foraging height was highest in the Coal Tit and Varied Tit, lowest in the Japanese Bush Warbler, and intermediate in the Red-billed Leiothrix. Among the other small woodland birds, Varied Tits and Coal Tits foraged in the highest layer, Willow Tits and Great Tits in the intermediate and lower layers and Long-tailed Tits foraged at a wide range of heights. Despite limited sample sizes, a similar pattern in foraging has been observed in other regions of Kyushu where Leiothrix has invaded (e.g. Mt. Hikosan and Mt. Ichibusayama, Eguchi & Masuda 1994; Kikuchi Glen, pers. obs.).

Data on the utilization pattern of foraging space among small woodland birds during the breeding season are limited outside Kyushu (but see Nakamura 1970; Ogasawara 1975). There is, however, a similar pattern of foraging space use among Paridae and other small woodland species during the breeding season in various areas in Japan; e.g., Kyushu (this study), central Japan (Nakamura 1970) and northern Japan (Ogasawara 1975). For example, Varied Tit and Coal Tit forage in the upper layer of the forest, while Great Tit and Willow Tit forage in the middle and/or lower layers. Long-tailed Tit has a broad foraging range, but is found especially in the lower layers of deciduous broad-leaved trees and in the middle and higher layers of coniferous trees in a mixed forest with sparse undergrowth, in central Japan (Nakamura 1970). Given the similarities in the use of foraging space between this study (where Leiothrix occur) and those elsewhere, it appears that there is no distinct shift in use of foraging space in any species in the presence of Leiothrix. Hence, it is unlikely that the segregation in use of foraging space observed among species in Kyushu has been brought by interspecific competition with introduced Leiothrix.

Ecological segregation can be achieved by employing unique foraging techniques, such as jumping to capture prey, which is commonly used by the Red-billed Leiothrix, but rarely used by other species. Leiothrix flies quickly from branch to branch, whereas tits and bush warblers hop or walk relatively slowly in the foliage (pers. obs.). Such movement is related to the main foraging techniques adopted by each species. It is likely that the foraging space utilization and the foraging technique of the Red-billed Leiothrix are both well adapted to foraging for aerial insects or agile invertebrates on leaves and twigs. Indeed, this species often provided aerial insects such as Mecoptera to its nestlings (pers. obs.).

In contrast to Leiothrix, Paridae species foraged exclusively by gleaning and hanging, which suggests that these species adopt a foraging technique suitable to capturing prey of low mobility such as Lepidoptera larvae on leaves and twigs. In southern Japan, Great Tit and Varied Tit mainly feed Lepidoptera larvae and spiders to their nestlings (Eguchi 1980, 1985). These relatively inactive prey items can be captured easily by gleaning. Tits and bush warblers are less able to capture aerial prey even when it rests on a leaf or twig. Gleaning is also the common foraging technique reported for Paridae and Long-tailed Tits in other areas, whereas jumping to capture prey is rarely reported (Nakamura 1970, 1978; Ogasawara 1970, 1975).

2) Morphological constraints

Morphological characters are closely related to ecological characters in some restricted taxa (Leisler & Winkler 1985; Wiens 1989). Morphological constraints may restrict the range of foraging techniques adopted by any given species. A long bill, for example, is suitable for capturing and firmly grasping aerial insects or those of high mobility, while short bills are found predominantly among gleaners (Leisler & Winkler 1985). The Red-billed Leiothrix has a long bill in comparison with other sympatric species, except for the Japanese Bush Warbler. While on the one hand the Red-billed Leiothrix has a relatively wide tail and the extremities of the outermost rectrices curve outwards, which may enhance its manoeuvrability in the air, on the other hand, its large dumpy body may be less suited to moving among leaves for gleaning. Shorter wings relative to body weight of Leiothrix (see Appendix) are not suited to hawking aerial insects in the air, either. The Japanese Bush Warbler has a long bill and long tarsi, as does Leiothrix, but the bush warbler has a rather slender body, which is perhaps related to its habit of clinging to stems of dwarf bamboo. Indeed, the bush warbler foraged exclusively in dwarf bamboo during this study. Thus, due to morphological constraints, the foraging space and foraging technique of the Red-billed Leiothrix were quite different from both the Japanese Bush Warbler and Paridae species. Because the difference in foraging pattern was great, it is unlikely that there is severe interspecific competition for food resources between the Red-billed Leiothrix and native species.

3) Invasion by the Red-billed Leiothrix

Eguchi and Masuda (1994) showed that the Red-billed Leiothrix mainly inhabits deciduous broadleaved forests with dense dwarf bamboo in the understory in Kyushu, and that its foraging microhabitat is segregated from those of sympatric species. They speculated that the poor species diversity in the avifauna in the lower, shrub layer of the forest is one of the factors contributing to this species' successful invasion and range expansion in Kyushu. In this study too, the Red-billed Leiothrix was found to mainly forage in the lower layer of the deciduous broadleaved forest with dwarf bamboo in the understory.

Sampling of invertebrates with sticky traps revealed that the abundance of aerial insects tended to be higher in the lower layer of the forest just above the dwarf bamboo canopy, than in the upper layer. In such a foraging space, Leiothrix captured aerial insects by jumping. Although other species, such as Long-tailed Tits and Willow Tits, often foraged in the same foraging space, they seldom used jumping as a foraging technique. The Japanese Bush Warbler mainly foraged at lower heights than Leiothrix and seems to forage primarily in dwarf bamboo, being found there in most of our observations. Even when they occur in the same foraging space, Leiothrix and Paridae species may prefer different prey. The food resource just above dwarf bamboo, consisting mainly of aerial insects, may be a reserved resource for the Red-billed Leiothrix.

In central Japan, there are many species specializing to foraging aerial insects such as *Muscicapa* flycatchers, Narcissus Flycatcher *Ficedula narcissina*, Blue-and-white Flycatcher, Paradise Flycatcher *Therpsiphone atrocaudata*, etc. (Agency of Environments 1981; Ornithological Society of Japan 2000). These species mainly capture aerial insects in the intermediate vegetation layer of the forest or among the tree canopy. Only one of these species, however, the Blue-and-white Flycatcher, preys on aerial insects in the forests where the Red-billed Leiothrix has invaded in Kyushu (Eguchi & Masuda 1994, pers. obs.). We postulate that the Red-billed Leiothrix has successfully invaded and increased in deciduous broadleaved forests in Kyushu, by virtue of the relatively low diversity of sallying and hawking bird species foraging for aerial insects in such habitats.

In this study, we found no evidence of any severe direct interspecific competition between introduced

Red-billed Leiothrix and native species. Amano and Eguchi (2002) have suggested, however, that indirect interference may occur, through increase numbers of Red-billed Leiothrix drawing predators to dwarf bamboo, a habitat in which the Japanese Bush Warbler nests, and that increased visits by predators may result in lowered breeding success of the Japanese Bush Warbler. Further studies on the interactions between invasive and native species, including field experiments such as the removal of dominant species (Martin & Martin 2001), are needed.

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REFERENCES

Alatalo RV (1981) Interspecific competition in tits *Parus* spp. and the goldcrest *Regulus regulus*: foraging shifts in multispecific flocks. Oikos 37: 335–344.

Ali S & Ripley SD (1972) *Handbook of the Birds of India and Pakistan*. Vol 7. Oxford University Press, Bombay.

Amano HE & Eguchi K (2002) Nest-site selection of the Red-billed Leiothrix and Japanese Bush Warbler in Japan. Ornithol Sci 1: 101–110.

Case TJ (1996) Global patterns in the establishment and distribution of exotic birds. Biol Conserv 78: 69–96.

De Schauensee RM (1984) *The Birds of China*. Oxford University Press, Oxford.

Eguchi K (1980) The feeding ecology of the nestling great tit, Parus major minor, in the temperate evergreen broadleaved forest. II. with reference to breeding ecology. Res Popul Ecol 22: 284–300.

Eguchi K (1985) Food size, energy intake and nutrient intake of nestling tits, *Parus varius* and *Parus major*. J Yamashina Inst Ornith 17: 74–83.

Eguchi K & Amano HE (2000) Problems in introduction of birds. J Conserv Ecol 5: 131–148 (in Japanese with English summary).

Eguchi K & Masuda T (1994) A report on the habitats of Peking Robin *Leiothrix lutea* in Kyushu. Jpn J Ornithol 43: 91–100 (in Japanese with English summary).

Environment Agency of Japan (1981) *Nihonsan Chourui no Hanshoku Bunpu* (Atlas of Breeding Birds in Japan). In: *A Report of 2nd National Census for Wildlife Conservation*. p 554. Publication Division of the Ministry of Finance, Tokyo (in Japanese).

Gibb J (1954) Feeding ecology of tits, with notes on treecreeper and goldcrest. Ibis 96: 513–543.

Herrera CM (1978) Niche-shift in the genus Parus in southern Spain. Ibis 120: 235–240.

Hogstad O (1978) Differentiation of foraging niche among tit, *Parus* spp., in Norway during winter. Ibis 120: 139–146.

Jones C (1996) Bird introductions to Mauritius: status and relationship with native birds. In: Holmes JS & Simons JR (eds) *The Introduction and Naturalisation of Birds*. pp 113–123. Stationery Office Publish Centre, London.

Lack D (1971) *Ecological Isolation in Birds*. Harvard University Press, Cambridge.

Leisler B & Winkler H (1985) Ecomorphology. In: Johnston RF (ed) *Current Ornithology* Vol 2. pp 155–186. Plenum, New York.

Lever C (1987) *Naturalized Birds of the World*. Longman, London.

Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evol 8: 133–137.

Long JL (1981) *Introduced Birds of the World*. Reed, Wellington.

Long Z (1987) Leiothrix. In: Chen T, Long Z & Zheng B (eds) *Fauna Sinica*. pp 154–162. Science Press, Beijing (in Chinese with English summary).

MacKinnon J & Phillipps K (2000) *A Field Guide to the Birds of China*. Oxford University Press, Oxford.

Martin PR & Martin TE (2001) Ecological and fitness consequences of species coexistence: a removal experiment with wood warblers. Ecology 82: 189–206.

Morse DH (1978) Structure and foraging patterns of tit flocks in an English woodland. Ibis 120: 298–312.

Moulton MP (1993) The all-or-none pattern in introduced Hawaiian Passeriformes: the role of competition sustained. Am Nat 141: 105–119.

Moulton MP & Pimm SL (1983) The introduced Hawaiian avifauna: biogeographic evidence for competition. Am Nat 121: 669–690.

Mountainspring S & Scott JM (1985) Interspecific competition among Hawaiian forest birds. Ecol Monogr 55: 219–239.

Nakamura T (1970) A study of Paridae community in Japan. II. Ecological separation of feeding sites and foods. Misc Rep Yamashina Inst Ornithol 6: 141–169 (in Japanese with English summary).

Nakamura T (1978) A study of Paridae community in

Japan. IV. Ecological segregation of species by the difference of use of bill in space and technique. Misc Rep Yamashina Inst Ornithol 10: 94–118 (in Japanese with English summary).

Ogasawara K (1970) Analysis of mixed flocks of tits in the Botanical Garden of Tohoku University, Sendai. II. Foraging layers by species and their interrelations within the mixed flock. Misc Rep Yamashina Inst Ornithol 6: 170–178 (in Japanese with English summary).

Ogasawara K (1975) Analysis of mixed flocks of tits in the Botanical Garden of Tohoku University, Sendai. IV. Foraging habits and supplanting attacks among species forming mixed flocks. Misc Rep Yamashina Inst Ornithol 7: 637–651 (in Japanese with English summary).

Ornithological Society of Japan (2000) *Checklist of Japanese Birds* 6th ed. Ornithological Society of Japan, Obihiro.

Sol D, Santos DM, Feria E & Clavell J (1997) Habitat selection by the Monk Parakeet during colonization of a new area in Spain. Condor 99: 39–46.

Tojo H (1994) Population increase of the Red-billed Leiothrix *Leiothrix lutea* in the Massif Tsukuba. Jpn J Ornithol 43: 39–42 (in Japanese with English summary).

Wiens JA (1989) *The Ecology of Bird Communities*. Vol 1. *Foundations and patterns*. Cambridge University Press, Cambridge.

Appendix. Measurements of body size for each species studied. Means with SD are shown. Males and females of Japanese Bush Warblers are shown separately because of a great sexual dimorphism in size.

Species	N	Wing length	Tail length	Tarsus length	Bill length	Body weight	WL/log (BW)	TL/log (BW)	TRL/log (BW)	BL/log (BW)	WL/TRL
L. lutea	222	67.3±2.5	58.5±2.4	24.8±1.1	15.8±0.9	21.9±1.3	21.8±0.8	19.0±0.8	8.0±0.4	5.1±0.3	2.7±0.1
C. diphone male	14	65.6±2.0	67.0±3.6	25.0±1.2	5.6±2.1	18.5±1.5	22.5±1.1	23.0±1.5	8.6±0.4	5.4±0.7	2.6±0.2
C. diphone female	18	53.8±3.3	53.7±6.0	22.5±1.7	5.5±2.4	11.5±1.5	22.1±1.4	22.1±2.3	9.3±0.7	6.4±1.0	2.4±0.2
A. caudatus	5	55.2±1.3	65.8±12.6	17.1±1.1	8.6±1.3	8.1±1.3	26.6±1.4	31.9±7.4	8.3±1.0	4.1±0.3	3.2±0.3
P. montanus	3	57.7±7.1	54.3±3.2	17.3±1.5	10.8±0.4	10.9±0.8	24.2±2.7	22.8±1.7	7.2±0.7	4.5±0.1	3.3±0.2
P. major	12	65.1±2.5	58.5±5.9	19.3±2.0	11.4±0.9	14.1±1.1	24.6±1.0	22.1±2.1	7.3±0.9	4.3±0.3	3.4±0.3
P. ater	6	59.4±4.6	46.1±5.1	16.9±1.5	9.8±1.2	9.2±1.2	26.9±2.2	20.8±1.4	7.7±0.6	4.4±0.6	3.5±0.4
P. varius	8	75.5±4.4	54.3±4.1	19.3±1.0	13.0±0.9	16.6±0.8	26.9±1.5	19.3±1.4	6.9±0.4	4.6±0.3	3.9±0.3